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# THE INFLUENCE OF CONTEMPORARY MAN ON THE ZOOGEOGRAPHY OF THE PANAMA LAND BRIDGE, PANAMA (U)

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## ABSTRACT

The biophysical geography of the Republic of Panama is summarized. There are detailed discussions of pre-historic and historic human ecology on the isthmus with emphasis given to exploitive activities and how they relate to biotic disturbances and alterations. It is shown that man must have been in the isthmian area nearly 20 thousand years ago and that his activities, first as a food gatherer and later as a food producer and gatherer, have markedly influenced the vegetation cover and the faunal patterns on the isthmus. It is posited that the environmental influence was sufficiently great in pre-historic times to have played a significant role in certain faunal dispersals over the land bridge which connects North and South America. The Spanish invasion in the 16th century resulted in a drastic decrease in human population which led to the reestablishment of forest cover over large parts of the isthmus and, probably, an alteration of some of the faunal patterns which obtained at the time of European contact. The imposition of new land-use patterns and the growth of human populations in recent years have led again to major tree removal and faunal impoverishment. The redistribution of human population particularly in the region of the Canal has resulted in major forest removal and the creation of a new barrier to the dispersal of certain forest faunal elements. On the other hand, the changed conditions have favored the dispersal of faunal elements which are adapted to grass lands and/or second growth conditions.

# INTRODUCTION

The study which follows is an attempt to show that man has been a biogeographic factor on mainland Middle America for a period of time approaching twenty millenia.

When the investigation was first undertaken it was to have been limited to an evaluation of human-influenced zoogeographic changes on the Panama Land Bridge during the twentieth century. However, during the course of the field study it became increasingly obvious that the scope of the investigation was too limited in its time depth. This fact became increasingly apparent when an analysis of the field data began. Thus, it was decided to extend the study to include the entire period during which man seems to have been present in the isthmian region. The writer is grateful to the Office of Naval Research for permitting him added time to pursue the extended line of investigation.

The ecological role of man in the humid tropics of the Western Hemisphere is very inadequately understood and there persists in several scientific quarters the notion that, in the main, the forests of Neotropica are "forests primeval." Though written four decades ago the following statement might still identify the ideas held by rather too many scientists-scholars as to the past role of man in one part of Neotropica, the isthmus of Panama:

> Human occupation of Panama to a degree sufficient to exert a marked effect on the original biota is still restricted largely to particular sections leaving the greater part of the region in primeval condition. (Goldman, 1926)

Though the study to follow is only introductory and exploratory in nature the writer hopes that all who read it will come away with

an appreciation of the role of humen cultural activities in shaping or influencing the faunal patterns of mainland Middle America. By extrapolation, it should also become apparent that all areas within the humid tropics of the world must be examined with the end of discovering to what degree the assumed pristine ecological conditions are in fact the result of human cultural machinations.

* * * * * * *

In most cases maps pertaining to particular parts of the text are mentioned in appropriate p'aces but two exceptions should be noted, (1) the location map of Panama - Map 10 - is not mentioned as this would entail too much repetition and the reader is advised to consult this map whenever an unfamiliar place name is mentioned, (2) the phytophysiognomic map of Panama - Map 4 - is mentioned in the first chapter but in Chapter 5 it would be very repetitious to do so and the reader is advised to consult the map when reading Chapter 5.

* * * * * * *

A field investigation invariably takes a heavy toll of kindness and cooperation from many persons and this study is no exception. It is not possible to express gratitude to all those who deserve it and the following list of persons include only those to whom the debt of gratitude is too great to go unexpressed here: Dr. Martin Moynihan, Director, Canal Zone Biological Area; Mrs. Adela Gomez, Administrative Assistant, Canal Zone Biological Area; Captain William Schweer, U.S.N., Commanding Officer, Fort Rodman, Canal Zone; Dr. and Sra. Aurelio Alba, Ocu, Panama; Don Jose Ferri, Aguadulce, Panama; Don Julio Afu,

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Chapter I

# BIO-PHYSICAL GEOGRAPHY

## Physiography

The isthmian link connecting North and South America, of which Panama is a significant part, did not exist throughout most of the Tertiary period when a water gap of indeterminate width prevailed. Exact determination of the times when the water gap first came into existence and when it disappeared is not yet possible but geological and paleontological evidence indicates that the gap was effective by the end of the Paleocene epoch and that a continuous land connection was established during the middle or late Pliocene epoch. Throughout most of the Tertiary period the region was subject to a high degree of active volcanism (Terry, 1956). Evidences of volcanism are extremely abundant in Panama and lend distinctiveness to many isthmian landscapes - particularly in the areas west of Panama City. Sedimentary rocks are abundant attesting to the long periods when parts of the present isthmus were beneath marine waters. Metamorphic rocks appear to be rare, at least in the surface geology.

The dominant physiographic feature of Panama is the western sierra which extends from Costa Rica into Panama eastward to within thirty miles of Panama City (Map I). Many local names are applied to this range and rather than repeat all of them here it seems useful merely to refer to the entire complex in Panama as the western sierra. It is composed largely, if not entirely, of volcanic materials and the dominant peaks are apparently all of volcanic origin, many being extinct volcanos. The highest of these peaks and the highest elevation in Panama is El Barú (or El Volcan)

and is located at the extreme western end of the range. This extinct (Pleistocene?) volcano rises to approximately 11,150 feet (3,427 m) and dominates the physical landscape of western Panama. A few miles to the east of El Baru, the second highest peak in Panama, Cerro Santiago, rises to 9,272 feet (2,852 m). Scattered throughout the length of the sierra are many unnamed peaks of volcanic origin. Eastward from Cerro Santiago elevations decrease in the sierra and then rise slightly at the eastern terminus where the plug forming Cerro Campana rises to 3,314 feet (1,000 m).

South of the western sierra and west of Panama City into Costa Rica there are numerous volcanic extrusives which form low hills, knobs, and caps. Dikes and plugs of varying size are also common in the sierran foothills. Volcanic ejecta covers large local areas as for example the Pacific slopes of El Baru and the southern slopes of the sierra just to the west of Cerro Campana. This last is a most conspicuous area and is the result of the deposition of material ejected from the crater of El Valle, an event which may have occurred in the Pleistocene (Terry, 1956). The materials have been deeply dissected to form extremely steep-sided interfluves almost barranca-like in form. The areal extent and depth (perhaps more than 150 feet, 46 m) of the El Valle ejecta suggests that at the time of the deposition a biogeographic event of considerable significance may have occurred, viz., the ejecta probably covered to lethal depths all the vegetation over many square miles from the sierra to the Pacific Ocean, filled all the water courses, and destroyed all animal life not able to flee. After the event it is likely that the disturbed area acted as an important barrier to biotic dispersal through this part of the isthmus. Indeed, it may still be a partial barrier.

A second prominent physiographic feature of western Panama is the Azuero Peninsula which thrusts southward into the Pacific. Low on the north its elevations rise in the southwest and culminate at just above 6,000 feet (1,846 m) at the top of the little-known Cerro Cambutal which is probably of volcanic origin. It lies in a knot of peaks that are usually obscured by clouds and mists making observation from the air all but impossible. It is possible that much of the peninsula was an island during the Tertiary but not, in this writer's opinion, since the Pliocene.

The area to the east of Panama City is somewhat less known than the western part just discussed. Perhaps it would be more correct to say that published materials are relatively scarce since several parts have received the attentions of petroleum exploration crews and thus the structure of some of the parts must be well known to a few persons. Physiographically the area seems to be in an older erosion cycle than is western Panama (Terry, 1956). Relief is in general more subdued than in the west with the highest elevation occurring along the Panama-Colombia border at the summit of Cerro Tacarcuna, 6,150 feet (1,850 m). The most extensively developed upland system, the serrania de San Blas, is aligned with the arcuate configuration of the Atlantic coast and has elevations ranging between 1,000 feet (300 m) and 2,000 feet (600 m). South of Cerro Tacarcuna and extending away from the Panama-Colombia border is an upland that reaches to just above a mile (1,620 m) at Cerro Pirre. Directly west from the last and close to the Pacific shore another small upland complex occurs which, at Cerro Jaque, reaches an elevation said to be one mile high (1,620 m). North of the last two named uplands and east of Panama City lies the remaining important upland in eastern Panama, the serrania de Maje, which rises to 4,720 feet (1,450 m). This is an all but unexplored region. The writer approached

it closely from the air and the summit area appeared to be of volcanic material.

Plain surfaces of low elevation are not common features in Panama and are almost confined to the Pacific side of the Isthmus. The most important development occurs in eastern Panama where broad arcuate valleys are occupied by the Rio Bayano and the Rio Chucunaque-Rio Tuira systems. In these areas the elevations are mostly below 600 feet (200 m). The second most significant plain is located west of Panama City and is centered in Cocle Province from whence it derives its name, the Llanos de Cocle. A plain of smaller extent has been developed at the Pacific foot of El Baru. The Atlantic coast is almost without plains because for much of its length low hills march down to the ocean. The chief exception occurs in the area adjacent to the Costa Rica border in the Province of Bocas del Toro.

The total land area of Panama has undoubtedly undergone considerable change during the geological past. The protean isthmus may have had a much smaller area than at present (Lloyd, 1963) but may have always followed its present sigmoidal orientation. With continued emergence and deposition the isthmus widened and at times may have been much larger than at present especially during the Pleistocene when sea stands were below the present. Tuan (1960) has presented evidence to show that sea stands were at least 80 feet (24 m) lower than now and it appears that world-wide sea stands were at times 300 feet (100 m) lower than now (Flint, 1957). A lowering of sea stands would have most importantly effected the Pacific side where the continental shelf extends well offshore on the Golfo de Panama and Golfo de Chiriqui areas. Maximum lowerings would have joined the Perlas Island group to the mainland as well as Isla Coiba (providing isostatic conditions prevailed).

A further note of physiographic significance is the lowest elevation along the continental divide. This presently occurs in the region of the Canal Zone a few miles north of Panama City and is approximately 200 feet (61 m) in elevation. The cutting of the Canal has in fact lowered the elevation to approximately 37 feet (25 m) which is the level of the man-made Gatun Lake. If there has not been any significant earth movement in this area since the isthmian link came into existence, this low elevation has been of great significance in the past as it must be at present to biotic dispersals across the isthmus.

## Climates

Present zoogeographical patterns on the isthmus of Panama and in contiguous regions argues for climatic changes during and after the Pleistocene. Paleoclimatic reconstructions for the isthmus can scarcely be said to have begun but some light is cast on the matter by data from Colombia and Costa Rica.

Results obtained from pollen samples taken in soundings in northern Colombia indicate that significant altitudinal shifts in temperature occurred during the late Wisconsin (Würm)glaciation (van der Hammen, 1961). In Costa Rica an analysis of pollen samples obtained at 9°43'N 83°56'W indicates an altitudinal shift downward by 2,112 feet (650 m) of the tree line during the latter part of the Wisconsin glaciation (Martin, 1964). Weyl (1955) reported on geomorphic signs of glaciation in the Sierra de Talamanca at points not far removed from western Panama. It is not yet possible to assign reliable estimates to the magnitude of the indicated temperature changes but they would appear to be of importance to biotic dispersals.

Contributing to the hypothesis that there were significant altitudinal lowerings of temperatures on the isthmus of Panama during the Pleistocene are some aspects of present and past mammalian distributions on the isthmus and in areas to the north and south which strongly suggest that conditions now obtaining at elevations between 4,000 feet (1,230 m) and 6,000 feet (1,845 m) were once reduced to near sea level. One example is the present distribution of the shrew genus Cryptotis which is of a very disjunct nature on the isthmus of Panama and Central America. If temperature is a prime controlling factor in the distribution of this insectivore it would require a marked lowering of temperature to permit it to disperse across the lower parts of the isthmus.

The present arrangement of macroclimates are fairly well known or may be interpolated with a fair degree of accuracy (Map 2). For descriptive purposes the widely employed Köppen climatic classification will be used in the discussion to follow but it should be kept in mind that this classification, like most others, suffers in terms of its direct applicability to biogeographic phenomena. This is due largely to the fact that its regional generalizations are derived from arithmetic mean values of climatic elements in turn derived from weather data obtained from instruments that seldom are placed in characteristic biological situations.

The latitudinal position of Panama imposes upon most of it an alternation of "wet" and "dry" seasons. Although some authors have treated these seasonal changes as though they occur with a chronometer-like regularity, exactly the opposite is usually the case. An examination of rainfall data for almost any station on the isthmus reveals that rainfall variability is great and may be of far reaching biogeographical significance (Bennett, 1963). A further problem is presented by the use of the

adjectives "dry" and "wet". It seems doubtful that any fixed and generally applicable quantity of precipitation can be assigned to either of the adjectives at least insofar as biogeographic applications are concerned.

In the Köppen system a tropical warm (A) climate is said to be continuously moist (f) if the average precipitation of the dryest month is not less than 2.4" (60 mm) - such a climate is termed a tropical rainforest climate. An area of A climate having at least one month with an average precipitation of less than 2.4" may, if there is heavy precipitation later in the year, be designated as tropical monsoon climate (Am). The Af/Am boundary is determined by application of a formula based upon the total precipitation received in a calendar year which is compared with the amount of rain which falls during the driest month(s). The idea is that copious rainfall can have a compensating effect on the period of reduced precipitation. Whatever value such a conclusion may have for descriptive climatology it must have little or no application to the facts of biotic distributions. A periodic shortage of environmental moisture, as a shortage of any other necessary ecologic component in an environment, can scarcely be compensated for if certain living organisms cannot continue to function during the period of shortage, as per Liebig's law of minimum. Other areas in the A climates with dry months as defined by Köppen but which do not have the so-called compensating rains at other times are termed tropical savanna climates (Aw). It might be further indicated that the traditional use of calendar months in climatology tends to obscure the actual duration of wet and dry periods however they may be defined. The foregoing caveats notwithstanding, the Köppen system provides the biogeographer with a useful means of grossly depicting the broad regional configurations of

macroclimates in any area and is superior to some of the more misleading climatic designations which have commonly appeared in the biogeographic literature.

In Panama the wet season usually occurs between late April to middle December with the dry season occurring during the remaining period. The intensity in the development of the two seasons varies markedly in different places over the isthmus. The dry season has its best development in areas from Panama City westward and south of the western sierra. The moistest dry season areas are found on the Atlantic slopes and at the higher elevations on the isthmus. The onset of the dry season is heralded in a typical year, by the sudden appearance of the northeast trade winds which, in their passage over the land, describe fairly intricate local patterns because of the alignment of highlands athwart the wind's path. In the Cocle Plains area the winds are exceedingly well developed and their searing effect is often felt for four months each year. In the region of the Canal Zone, where there is a minimum of obstruction, the winds often sweep past with great vigor passing over the Golfo de Panama with sufficient frictional drag as to produce upwelling in the marine waters (Schaefer and Bishop, 1958). In the upper elevations of the western sierra the winds blow with great force forcing clouds and mists along in a wild profusion. In other parts of Panama, as for example in the northwest end of the Azuero Peninsula, the trades seem to be weakly developed near the ground.

The wet season usually arrives accompanied by increases in atmospheric humidity and, in the beginning, temporary suspensions of the trade wind flow. Convectional activity increases rapidly and heavy rains become frequent. After the wet season is well developed wind directions alter and strong south winds accompanied by heavy precipitation are a common

feature. Much electrical activity accompanies the wet season disturbances.

Climates of the highlands are modified by the temperature lapse rate of the atmosphere. The alignment of the highlands also tends to create important quantities of orographic precipitation ar almost daily mists are the rule over the higher points. In the El Baru area a common dry season phenomenon on the Pacific side are light mists, bajareque, which fall from cloudless skys having been driven over and past the summit areas by the trades. Although the areal extent of the highland climates (designated as Cw on the map) is based largely upon assumptions of lapse rates and seasonal patterning (summer) of precipitation, it is believed that they are approximately correct.

## Hydrography

With the partial exception of the Rio Chagres, all the large rivers of Panama drain to th_ Pacific. The Chagres once drained to the Atlantic only but now its waters are employed in Canal lock operations which means that some of the river's waters find their way to the Pacific. Because of the limited land area there is a paucity of well developed drainage systems - in fact only two significant river systems exist, viz., the Rio Chucunaque-Rio Tuira and the Rio Bayano (Map 3).

The markedly seasonal aspect of precipitation over much of the isthmus greatly influences the stream flow regimes. Durin, the rainy season river flow is at a maximum and floodin, is a common phenomenon with most of the rivers carryin, a heavy silt load. Durin, the drier period the rivers often fall very low and otherwise turbid streams often flow clear. This last being especially true of the tributary streams of the Rio Bayano and Rio Chucunaque. The latter river remains murky with

its silt load throughout the year although tne Bayano usually becomes very clear during the dry season. The alternation of murkiness and clarity is characteristic of many of the streams in western Panama such as the Rio Santa Maria and Rio Chiriqui Viejo. Some small streams such as the Rio Ancon in western Panama have a permanent discoloring of their waters due to the passage of their waters across volcanic tuffs which in the case of the just named stream imparts a milky appearance to the water throughout the year. In areas where there has been serious forest removal stream flow regimes are seasonally very dissimilar. In such cases rainy season flooding alternates with dry season flows which may be so reduced as to cause the streams to be no more than a series of pools joined by small trickles of water.

Lakes are by no means common in Panama with the only large ones - Madden and Gatun - being of human construction for Canal operation. A lake of a few acres extent occurs in the El Hato area on the slopes of El Baru at just above 4,000 feet elevation. A lake formerly existed in the caldera crater of El Valle but was long ago drained when the headward cutting Rio Anton breached the crater's south wall. A very small lake - Laguna de Las Yeguas - lies in the sierran foothills north of Aguadulce in central western Panama. There is also a very small lake on Cerro Tacarcuna. Aside from the above mentioned modest entities no other natural lakes in Panama are known to this writer. Oxbow ponds are a common feature of at least the lower two thirds of the Rio Chucunaque and extensive marshy areas occur in the lower portions of the same river. On older maps the area is shown as a lake - la Laguna de Matusagrati - but this is in fact only a seasonally flooded area, not a lake.

## Phytophysiognomy

In the belief that it is the phytophysiognomic rather than the floristic characteristics of vegetation that are of the greater significance to animal distributions and dispersals the remarks to follow will be chiefly confined to the physical appearance of isthmian vegetation.

Several systems of phytophysiognomic classification are available but all require some revision when employed in the field. The system that this writer has found to be most applicable to general conditions in Panama is one devised by Beard (1955). However, Beard's classification does not allow for major considerations of human influences on vegetation and furthermore carries with it a too heavy implication that climaxes are the rule. Thus, while the phytophysiognomic units recognized by Beard do in fact exist this writer finds himself reluctant to employ his terminology since to do so would be to strongly imply that the present facts of phytophysiognomy on the isthmus are "natural" or pristine when it is a major purpose of this paper to demonstrate just the opposite. Therefore in a desire to focus attention upon the human altered aspects of isthmian vegetation Beard's useful classification is not here employed but instead one devised by the writer is used. The following remarks are designed to supplement the map legend. (Map 4).

Old Mature Forest. While it is not possible to assign an age to this formation it is probably close to a climax situation - if there is such a phenomenon as climax vegetation. It is located almost entirely in the upper elevations of the various large and small sierras of Panama which by virtue of elevation and the apparent lack of cultural artifacts indicating previous occupance by man is here judged to have been the object

of virtually no alteration by man in the past. Areas above 5,000 feet generally experience markedly humid conditions throughout the year - this is particularly true of the upper regions which receive the full blast of the trades. With the exception of the El Baru region these highland forests are little known at present.

Old Forest. This formation occurs at present where historical or archaeological records indicate previous human occupance at the agricultural level. Today such areas are all but vacated by man which is a post-contact phenomenon.

Forest. This formation is very similar to the one just described but differs chiefly by being disturbed at present (and probably also in the aboriginal past) by the cultural activities of man. Sufficient areas in forest remain to justify inclusion in this category although as in the areas adjacent to the Canal Zone but within the Republic of Panama the forest is now reduced to isolated patches which in themselves will probably cease to exist in the not distant future.

Low Tress and /or Bush, Mostly non-Deciduous, Often Fire and Drought Resistent With Grass usually Abundant. This is a markedly culturally disturbed vegetation complex brought about chiefly through the activities of burning and overgrazing although it is likely that edaphic factors independent of the aforementioned also have been operative. A common shrub of the drier phase (4a) is Chumico, Curatella americana, which is often the first shrub-form to appear after a fire. Dense stands of this species occur in the Chiriqui area where they are given the name chumicales. (Chumico is also a common entity in map region 6a). Other characteristic taxa occurring in this formation are Nance, Byrsonima crassifolia, Marañon, Anarcardium occidentale, Malagueto, Xylopia spp., Cigua, Nectandra spp. Nance may well be the most abandant tree in this formation. The malagueto

is especially abundant in the 4a region of Chiriqui where it forms dense and almost pure stands on burned-over land. An abundant and frequent associate of the shrubs is the aggressive introduced grass, Faragua, Hyparrhenea rufa.

Thorn-Bush and Cactus. This formation seems to be under strong edaphic control, especially in western Panama. It is found just landward of mangroves (not mapped) and seems to occur on fairly saline and droughty soils. Since these areas are also subject to seasons of little or no precipitation this must also be a significant factor. Although man may not have played a significant role in creating this formation the possibility of man-set fires cannot be entirely ruled out as a contributing factor.

Many of the shrubs and trees are armed. Some of the many taxa present include Acacia, Hamelia, Oenocarpus, Prosopis, and the cactus Acanthocereus pentagonus. In the vicinity of Monagrillo (near Chitre) the writer discovered a species of Opuntia growing abundantly, but this may have been introduced. Its characteristics did not appear to agree with those given for O. elatior described from the Pearlas Islands. The Acanthocereus is chiefly located in the drier and more saline portions of this formation and sometimes occurs in the strand. The small area shown as 5 in Darien has been so designated on the basis of the shrub forms present which includes Prosopis.

Grass with isolated stands of trees and (often) Palms. This is a pronouncedly culturally induced formation and has usually come about where there has been a long history of burning and/or tree removal for agriculture and livestock grazing. In the moister areas, as for example near the Rio Santa Maria, woodland remnants are still common. In the drier areas the species composition is very similar to that of region 4 discussed above. Many of the woodland remnants now occur upon rocky outcrops formed by

the abundant volcanic extrusives alluded to earlier. Man-created palm savannas are common especially in the western end of region 6a and in 6b where the palms are spared for use as thatching material and for the fermentation of palm wine.

Grassy Plains. This formation has a fairly restricted distribution and has resulted from a congeries of edaphic, climatic and cultural factors. The formation is best developed in the eastern part of the Cocle Plain where soil conditions are very poor. During the annual dry season this area receives the full blast of the trades and also is set afire by deliberate and accidental acts of the human occupants. A surprising amount of shrub forms occur on which Curatella, Byrsonima, and Anacardium are most frequent. If burning were to be halted as well as all grazing most if not all of this area would revert to shrub and low trees.

Grass and/or Sedges on steep slopes. This formation owes its existence largely to long-repeated burning and forest clearing. The areas of major development are all in western Panama. In region 8a the appearance is one of considerable desolation - there being scarcely a tree upon the land. In region 8b there is a high component of sedges. In this last area a notable feature is the all but absent transition between the remaining forest and the grass and sedges. All of these areas would probably support tree cover providing there has not occurred some non-reversible edaphic change.

Galeria Forest. Only two instances of this formation are shown on the map because of the difficulty of showing it at reduced scale. These seem to be culturally induced phenomena being the stream-side remnants of once extensive woodlands or forests. Although taxonomically varied the more common taxa include Ficus spp., Anacardium excelsum, and Cecropia spp. The latter is also a common component of new second growth situations

in almost all parts of the isthmus.

Living Fences. This formation is not shown on the map because it is almost ubiquitous in the settled portions of Panama and occurs in such tenuous patterns as to preclude its mapping at the scale employed. Nonetheless it is an important phytophysiognomic feature and in many heavily settled parts of western Panama it constitutes the most conspicuous arboreal element. As the name implies, this formation consists of trees planted to form living fences for the purposes of fencing areas devoted to crops or livestock. Such a fence reduces termite damage which would rapidly result were dry timber to be employed. They also provide a wood supply for fuel and construction purposes. Many taxa are used but the following seem to be the most common, Bursera simaruba, Anacardium occidentale, Diphysa robinoides and Spondias spp. Sometimes, instead of trees, a terrestrial bromeliad, Bromelia spp., is employed. These are planted in dense thickets around house and garden sites to protect them from the unwanted incursions of livestock.

## Zoogeography

The importance of the area between Mexico and Colombia as a biotic land-bridge is well known and has been remarked and discussed too often in the literature to require any further exposition. On the other hand, many of the details - geographic, biotic, and historic - are still to be worked out and will occupy the time of many investigators in the years to come.

It is generally agreed that a water gap or gaps existed in the Panama - Central American region from the late Paleocene to the middle or late Pliocene thus resulting in a formidable ecological barrier between North

and South America during the greater part of the Tertiary. With the establishment of the land-bridge in the Pliocene there resulted a flow of mammalian taxa between the two continental masses with the more important flow being from north to south, i.e., the Holarctic invasion of Neotropica was the more important of the dispersals. (Simpson, 1950). However, in Recent time "the faunal flow has been entirely reversed" (Hershkovitz, 1958), and the mammalian fauna, at least, of the Central American-Panama bridge is today a Neotropical entity and not, as has been traditionally held, a transition zone between the Neartic and the Neotropical (Hershkovitz, 1958).

Sclater (1858) seems to have been the first to have assigned to this area the designation of a subregion of the Neotropical Region (on the basis of the avian fauna) and to have asserted that it was a transition zone. This designation has been generally followed to very recent time (Darlington, 1957) but insofar as mammals are concerned the designation is no longer justified. Until analysis of other faunal components (aves, reptilia, amphibia, etc.) are undertaken in the manner followed by Hershkovitz it seems appropriate to follow the latter for the time being inasmuch as most of the zoological observations in this section, as well as the entire study, are directed toward the mammalian fauna.

A careful examination of Hershkovitz's study suggests that a further refinement of geographic distributions than he achieved can be attained and that in so doing one may be able to show a greater degree of distributional complexity on the isthmus and Central America than was shown in the last cited publication.

In an effort to better illustrate this writer's later remarks, it is desirable to briefly review Hershkovitz's geographical sub-headings. Hershkovitz divided the pertinent mammalian distributions into geographic

groupings as follows:

| Holarctic | | Neotropical | | | |
|---|---|---|---|---|---|
| Nearctic | | Brazilian | | Pat | W. I. |
| No. | N.M. | S.M. | C.A. | Br. | |

No. = North America north of the Mexican boundary (i.e. the U.S.A. - Mexican political boundary)

N.M. = Mexico north of the Neotropical - Holarctic boundary (which appears to be drawn along the parallel of 23°30'N)

S.M. = Southern Mexico portion of the Brazilian Subregion (which apparently includes all of Mexico south of the Neotropical-Holarctic - Nearctic - boundary)

C.A. = Central American portion of the Brazilian Subregion (this includes Panama although elsewhere in the publication the Choco area of Colombia is included)

Br. = South American portion of the Brazilian Subregion (see Patagonian Subregion, i.e., this includes those parts of South America not in the Patagonian Subregion).

Pat. = Patagonian Subregion which "includes Uruguay, all of Argentina except Misiones and northern Corrientes, Chile, the alpine highlands of Bolivia, the coast and puna zones of Peru, the paramos of Ecuador to the equator, and the Falkland islands..."

W.I. = West Indian insular Subregion

Although the above geographic units served to demonstrate Hershkovitz's thesis that the area usually considered to be the Central American Subregion of the Neotropical is in fact (in terms of the mammalian fauna at least) only a northward extension of the Brazilian Subregion, a comparison of Hershkovitz's geographic units with a map will quickly show that the units are usually far from being any where near equal in area and thus, it is possible that some distributional complexities may be obscured. In an effort to demonstrate this last, the area between

45°N and 45°S have been divided into class intervals of 5° of latitude and the distribution of mammalian genera present in the areas have been plotted (Table 1). Hershkovitz's list of mammalian genera has generally been followed with some minor changes adopted from Hall and Kelson (1959) and Cabrera (1957, 1960).

An examination of Table 1 will permit one to perceive that there is a very considerable degree of mammalian distributional complexity in the Central American-southern Mexican area. The complexities suggest that there is reason to believe that there is little distributional stasis involved - rather the area may be supposed to be in a state of biogeographic flux. This seems to be no better illustrated than by the primates. On Hershkovitz's table the genera Cebus, Saimiri, Aotus and Saguinus occur in the Central American portion of the Brazilian Subregion. This strongly suggests that the ranges of all these genera are more or less equal throughout the entire area. However, Cebus ranges north as far as southern Honduras, Saimiri is confined to a small area of extreme southwest Panama and southwest Costa Rica, Aotus is not known west of the Azuero Peninsula in Panama and Saguinus does not occur north of Panama in the Central American area. The two remaining primate genera present in the area, Ateles and Alouatta, range north to southern Mexico with Ateles having the slightly greater northward extension. Had one degree of latitude classes been employed even more pronounced distributional variations would have been demonstrated.

It should also be noted that many of the mammalian taxa do not by any means have continuous distributions through the area. One example of many that might be cited is that of the shrew genus Cryptotis which has a markedly disjunct distribution through the Central American area being confined to isolated areas at moderate to high elevation.

Rather than treat in detail with the patterns of mammalian distributions in the entire Central American area, attention will be focussed upon Panama. To aid in describing the patterning of mammalian distributions in Panama the country has been divided into a series of 15' intervals of longitude. Longitude, rather than latitude is of the greater significance to biotic distributions in Panama due to the placement and configuration of the land mass. Panama extends through only slightly more than two degrees of latitude but through approximately six degrees of longitude.

In Table 2 are shown the distributions of mammalian genera (excluding chiroptera and marine genera) which are known to occur in Panama.

An examination of Table 2 will make it quite evident that very complex mammalian distributions obtain in Panama at present. It appears that the general area of the Canal Zone is the approximate westward limit of some forms, e.g. Hydrochoerus, the uplands of western and eastern Panama contain elements not common to the whole isthmus, e. g., Cryptotis, Macrogeomys; the Azuero Peninsula lacks some taxa which might reasonably be expected to occur there, e.g., Tapirus, Mazama; western Panama is the southward (and eastward in Central America) limit of some taxa, e.g., Jentinkia. The Boquete area seems to contain an especially distinctive mammalian fauna which includes some forms not known to occur elsewhere in Panama, e.g., Syntheosciurus, Reithrodontomys sumichrasti, Scotinomys xerampelinus, Rheomys hartmanni.

The insular mammalian faunal assemblages are fairly well known. The largest island group, Archipielago de las Perlas, lies in the Golfo de Panama distant approximately 42 miles southwest of Panama City and approximately 20 miles distant from the nearest mainland (Darien). The intervening channel is within the 30 fathom curve. Isla Coiba, the largest island on the Pacific coast of Central America, lies to the west of the Azuero

Peninsula and just landward of the 50 fathom curve. Farther west there is a group of islands in the Golfo de Chiriqui which appear to have only recently come into existence as a result of either land subsidence or a rise in sea level. During low tide periods some of the islands coalesce to form larger units. The greater part of the surfaces of these islands are effected by daily tidal changes. The channels are very shallow - only a slight lowering of sea level would reunite all of them with the mainland. Approximately one mile south of the last named group is Isla Boca Brava and distant from this last at about 4.5 miles is Isla Parida.

On the Atlantic side there is a series of islands in the Laguna de Chiriqui-Bocas del Toro area, all within shallow water. Approximately 14 miles offshore is the small and isolated Isla Escudo de Veraguas. No other islands are to be encountered until east of the Canal Zone where there is stretched along the coast a series of coral islands of small individual size.

In Table 3 are given the distributions of mammals for the islands as presently known and, in a few cases, the avian distributions are also considered. The mammalian fauna of the Chiriqui Islands is obviously derived from the very adjacent mainland. The Coiba Island mammalian assemblage is extremely peculiar having an unexpectedly great paucity of taxa. The mammalian fauna of the Islas Perlas suggests that the group has at one time been joined to the mainland but this does not answer some of the questions posed. Why, for example, does Mazama only now occur on S n Jose but is not known from the larger Isla del Rey? Why does Mazama occur there instead of Odocoileus? Some partial and tentative answers will be offered below in sections dealing with cultural influences.

## Biophysical Regions

Various biologist, geologists, and geographers working in Panama have over the years sought to generalize the facts of the distribution of physical and biological phenomena onto regional maps. An early attempt to construct such a regional map was that accomplished by a Colombian geographer (Perez, 1863) who divided the isthmus into two longitudinal belts of which the northern was termed Selvas and the southern Sabanas. The over-generalized map is of no value now. The next, and thus far, the most influential regional scheme was proposed by Goldman (1920) who divided the isthmus into a series of life zones which were as follows: "beginning at sea level these are the Lower Tropical Zone, of which there are well-marked arid and humid divisions; the Upper Tropical or Subtropical Zone, and the Temperate Zone."

Without going into great detail as to where the several zones were located it is important to point out that the use of such designations as "arid", "temperate' and "subtropical" is not justified in Panama. Goldman noted in the descriptions of his zones that the so-called arid portions had heavy seasonal rains but still chose to use arid because of the season of little or no rains which also occurred in the same areas. Arid should be reserved for use in desert situations, some of which are of course tropical in their latitudinal distributions. The term temperate which comes so ready to the pen is another one that should usually be avoided unless there is an accompanying careful description of what the author means by temperateness. Although the question of temperateness of climate has recently received important treatment (Bailey, 1964) its casual use, particularly insofar as tropical highlands are concerned, is not, in this writer's view, justified. The term subtropical also is too

general to be of much assistance in comprehending just what sort of climatic situation is being indicated. The same term is often applied to the Cs climates (Mediterranean) of the Koppen system as well as to some Cfa climates in the same climatic classification. In Panama, Goldman applied subtropical to elevations of 3,000 feet to 8,500 feet.

Goldman was handicapped in not having weather data available and in not having visited many important parts of the isthmus. He also was of the opinion that he was describing essentially pristine conditions as the following quotation will illustrate 'Excepting at the Canal Zone and limited areas in western Panama the republic is sparsely populated by man; clearings are few, and aside from the rather extensive, open, grassy savannas near the Pacific coast and smaller grass areas in the Chagres Valley, the isthmus is a practically unbroken expanse of forest." In a later publication (1926) Goldman reiterated his position thus: "Human occupation of Panama to a degree sufficient to exert a marked influence on the original biota is still restricted largely to particular sections leaving the greater part of the region in primeval conditions. These postulates will be challenged later in this paper so here attention is directed to the fact that Goldman's life zone construct for Panama requires, in any case, some important modifications in terminology and construction. In the absence of any other regional scheme we find many authors following Goldman as for example Aldrich and Bole (1937) who, in an investigation of birds and mammals of a small part of the Azuero region, fit Goldman's classification into their area. Thus we find an area that is actually an Am (tropical Monsoon) climate being described as a part of the arid division of the tropical zone. A paper by Breder (1945) dealing with the amphibians and reptiles of Darien also follows Goldman's scheme even going so far as to extend the arid division up the Rio Chucunaque some

distance beyond the Rio Tuquesa. All of this area is certainly within the Am climatic zone - to describe it as an arid region is to render the adjective meaningless.

Two more recent attempts to regionalize the isthmus are represented in the work of a pair of forester-ecologists (Holdridge and Budowski, 1956) and a geographer (Guzman, 1956). The former produced a map which showed the "plant formation" zones of the Republic of Panama. The effort has its chief value in being more sophisticated than Goldman's map but has the serious disadvantage of not having taken into consideration tree removal. Thus the map is essentially a reconstruction and does not at all represent current (and long past) conditions over much of the isthmus. The effort by Guzman resulted in a map which tries to unify the known facts of physical geography into a series of regions. In many respects this is the best map of its kind that has been produced for Panama but it has the serious fault of focussing upon the dry season so much as to use the term dry lands for some areas which is no better than the arid resignation of Goldman.

What appears to be the most recent attempt to divide the isthmus into some sort of biogeographic zones is that of Ryan (1963) who, using the biotic province concept of Dice, attempted to divide all of Central America into biotic provinces based upon an arithmetic analysis of mammalian groupings. Without embarking upon a criticism of the method employed by the author in his determination of the number and boundaries of the provinces he found to exist it is here noted that he divided Panama into three provinces, two of which are shared with Costa Rica. The limited criteria employed for the formulation of the regions makes its utility very reduced.

As a geographer, this writer is well aware of the usefulness of the regional generalization and does not depreciate its relevance to biogeographic representations. However, the writer does not believe that sufficient is known of the distributions of plant and animal taxa on the isthmus to justify an attempt to construct such a map at present. Goldman's quoted comments not withstanding, the isthmus has long been subject to the biotic disturbances of man and such disturbances will markedly increase in the future. Until we sort out the factors involved and the resulting alterations associated therewith it seems undesirable to attempt a life zone or biotic zone syntheses at this time. Of far greater use are individual maps that treat with individual geographic features, e.g., landforms, climate, vegetation, distribution of animal taxa, etc. Life zone maps have strong implication of fixity and climax which, on the isthmus at least, tend to lead biogeographical understanding astray.

Biologists and others will, nevertheless, find it almost necessary to relate their work to known facts of ecological geography on the isthmus. It is therefore suggested that the somewhat more laborious but more precise method of relating one's data to the individual and local facts of climate, landforms, hydrography, soils and so forth be followed. The isthmus of Panama is a small area but this should not continue to mislead field workers into the belief that the biophysical phenomena are simply grouped and easily depicted by cartographic techniques. Care should especially be given to the use of climatic terms. If an area has an annual season of reduced precipitation it is far more significant to attempt to indicate the quantities of precipitation involved and the calendric periods involved than to use the misleading adjectives alluded

to above. It is with the above in mind that the maps accompanying this paper have been drawn. It cannot be stated too strongly, however, that all the maps included herewith are provisional in nature and will necessitate major or minor revisions in the future as more complete data become available.

Chapter 2

# THE PRE-AGRICULTURAL PERIOD OF HUMAN OCCUPANCE

Archaeological data presently available provide only a few clues as to the time when the first humans arrived on and dispersed across the Central American isthmus into South America. The dating for the arrival of early man in North America has gradually been extended back to before 20,000 years BP with the present limit resting on a somewhat problematical date of 38,000 years BP - the Lewisville site in Texas (see Krieger, 1964, for a recent discussion of this site). Of very great importance are datings of sites in South America for these permit at least an approximation of the time span involved in the first human disperal - assuming that early man walked into South America. A not too firm date of approximately 20,000 years BP has been tentatively assigned to a site in south-central Colombia (Angulo Valdez, 1963, citing Burgl, 1957); a site in northern Venezuela has yielded a date of 16,000 ± 300 BP (Sanoja, 1963); a Lagoa Santa (Brazil, Minas Gerais) date of 10,024 ± 127 BP has been obtained (Krieger, 1964, citing Hurt, 1962); a date of 10,032 ± 400 years BP is associated with human artifacts in Mylodon Cave in the extreme southern part of South America (Krieger, 1964 - see also Bird, 1938). The foregoing is only a partial listing of carbon 14 dates now available for early man in South America but should serve to establish a gross approximation of the time depth involved, and makes it appear probable that between 15,000 to 20,000 years ago human groups were present on the isthmus of Panama.

The earliest (published) carbon 14 date available for Panama is 4,850 ± 100 BC (Lothrop, 1959, citing Deevey, et al, 1957) and relates to a pre-ceramic site in the central Coclé Plain (Cerro Mangote, see McGimsey, 1956 for an archeological description.) Thus it appears that something on the order of 6,000 to 14,000 years of pre-history preceded the earliest piece of physical evidence we now possess for the presence of man in Panama and of course the cultural level represented by Cerro Mangote can in no way be related to the cultural levels of the first peoples who entered the area or, probably, to many of the cultures present during some of the millenia prior to the developments associated with the Cerro Mangote site.

Thus it is obvious that any attempt to reconstruct the anthropogeography and ethnozoology of early man in the area must stem largely from conjecture. That the following discussion is in fact largely conjectural will be very apparent to the reader but it is offered as the only possible means by which some of the problems concerning this paper may be examined.

As is well known to students of New World pre-history, there is still lacking a generally agreed upon taxonomy of culture sequence. This of course presents a problem in communication and though it cannot at present be resolved the course adopted here is to use the stage or culture sequence terminology of more than one author and to cite each person as the term arises.

Pre-Projectile Point Stage (Krieger, 1964 = the Crude Percussion Industries of Willey, 1960; the Lower Lithic of Willey and Philips, 1958.) This appears to be the earliest identifiable culture level in the New World. Sites attributed to this technological level are

known in North America from south-central Mexico northward and from Venezuela to Tierra del Fuego in South America (Krieger, 1964.) Of the South American dates cited in the opening paragraph of this chapter the south central Colombia site is referable to this culture level (approximately 20,000 years BP.) Very little is known of the ecological relations of this stage. Willey (1960) has concluded that this stage probably had an unspecialized hunting and gathering economy but he is careful to note the necessarily very tentative nature of such a conclusion. These people possessed fire and a crude lithic industry which had not progressed to a point where serviceable projectile points could be crafted. Generalized gatherers operating in small groups may not have encountered serious ecological difficulties in dispersing across the isthmus if they stayed close to the marine littoral which would seem to have provided the richest and most easily exploited biotopes. One must wonder, however, as to what kinds of macroclimatic and vegetational conditions existed on the isthmus at at the time of first entries. If the conditions were essentially those prevailing today it seems that rather profound adaptations of shelter, food handling and preservation, and gathering techniques would have been required before successful dispersal could have taken place. There is also the question of a whole new series of pathological organisms to be faced which had not been present in middle and high latitude environments. Can it have been that very different climatic conditions existed then?

The arithmetic and physiologic population densities of these groups may be assumed to have been very low. The distribution of these people on the isthmus at any given time must have been extremely dispersed.

The effect that such cultures could have exerted on the ecology of the territory occupied must have been extremely modest. On the other hand, if these people regularly employed fire as a hunting tool, which seems entirely likely, the long time span involved suggests that the cumulative effects of burning might have been ecologically significant. It is not likely that their faunal exploitive efforts resulted in any important faunal changes, however.

Paleo-Indian Stage (Krieger, 1964 Pleistocene Big-Game Hunting of Willey, 1960). This stage apparently has its genesis in the U.S. southwest at around 15,000 BC (Willey, 1960) and may have been present in southern South America by 8,500 BC (Mylodon Cave). The economy of this stage was based upon hunting (Willey and Phillips, 1958) but must have included other subsistence activities as well. That such peoples dispersed across the isthmus is obvious but it is difficult to account for the reasons why hunters moved through the area at all. It may be assumed that "hunters of all ages from all cultures seemed motivated by a desire further to explore unspoiled hunting areas" (Birdsell, 1957) but anyone familiar with the modest hunting potential of the isthmus today - and the region north of the isthmus to Mexico - must wonder if the faunal conditions which were encountered by hunters were not markedly different than those which occur there today. The forested tracts on the isthmus of Central America do not presently support large mammalian populations - there is great taxonomic diversity but individual stocks tend to be small, particularly the stocks of the larger mammals such as tapirs (Tapirus) and brocket deer (Mazama). The populations of small mammals such as spiny rats (Proechimys) may be large in local areas but these small animals could hardly serve as the dietary support of people who were

chiefly dependent upon the chase for food and raw materials. In addition, it may be suggested that great uninterrupted tracts of tropical forests would have presented rather formidable barriers to hunters whose techniques had been fashioned in middle and high latitudes for hunting proboscideans (Mammut, Mammuthus) and bison (Bison) in fairly open country. At least two alternatives may be offered to account for the nature of the basic factors which made possible the dispersal of hunters across the isthmus of Central America into South America, viz., the geographic ranges of certain large Pleistocene mammals extended southward into Central America and perhaps beyond into South America, or the hunters modified their hunting techniques and general material culture to accomodate to humid tropical forest conditions. Let me briefly consider the first alternative.

A partial but fairly representative list of large mammals presumed to have been exploited by Pleistocene man in North America has been provided by Martin (1958). With certain revisions to bring the list into accord with Simpson's classification of mammals (1945) the more important genera include: moose, (Alces) Pleistocene to Recent, North America; pronghorn (Antilocapra) Pleistocene to Recent, North America; extinct "pronghorn" (Tetrameryx) Pleistocene, North America; whitetail deer (Odocoileus) Pleistocene to Recent, North and South America; bison (Bison) Pleistocene to Recent, North America; elk (Cervus) Pleistocene to Recent, North America; horses (Equus) Upper Pliocene - Pleistocene, North America, Pleistocene, South America; "camel" ( Camelops) Pleistocene, North America; "musk ox" ( Euceratherium) Pleistocene, North America; ground sloth ( Paramylodon) Pleistocene, North America; mastodon ( Mammut) Middle Miocene-Pleistocene, North America; mammoth ( Mammuthus) Pleistocene, North

America and possibly South America; mastodon ( Cuverionius) Upper Pliocene-Pleistocene in North America, Pleistocene in South America. (Paleontological occurrence from Simpson, 1945).

It appears that four genera from the list above might possibly have figured in Central America and Panama, viz., Odocoileus, Mammuthus, and Cuverionius. Of these four genera only Odocoileus occurs in a wild state today. If the extinct proboscideans just listed were present in the Central American area at the time of the first invasion by hunters, it could be surmised that hunters followed this choice game into South America. Unfortunately there is no cultural evidence that such was the case and even reported proboscidean material in Central America is extremely scarce. Mammoth ("mamut") teeth have recently been discovered in Costa Rica near the Pacific Ocean (Anon. 1963). Neither dating of the material nor its generic affinity have been reported in print so far as this writer can ascertain. However, let it be assumed that the four genera just mentioned were present in the area between Mexico and Colombia at the time the first hunters passed through. The limited land area involved would tend to preclude the presence of large numbers of any of the taxa. Furthermore, it is very likely that only the Pacific side (drainage) would have supported these animals. Whatever paleoclimatic and paleobotanic changes that might be involved for the area during the Pleistocene it is reasonable to assume that the Atlantic side would have been in heavy forest. This would be so unless there was a major change in world wind patterns and rainfall patterns on struck coasts. Thus a rather narrow Pacific corridor of woodland grass may have been the maximum ecological situation available for the occupation of the four taxa. That there have

long been forested conditions on the Atlantic slopes seems to be corroborated, in part, by the presence of such taxa as baird's tapir (Tapirus bairdii) whose range is limited today to the Central American Province of the Brazilian Subregion of the Neotropical Region. That the Pacific side was the likely route of passage for the early hunters seems likely in that the tapir has survived to the present in forested areas. If early hunters could be effective exterminators of large mammals in continental areas (see Martin, 1958) how much greater would their effectiveness have been on the constricted isthmus in question? Thus the survival of the tapir is strongly suggestive that the forest was not the route of dispersal. It might in turn be suggested that many of the-then-present large mammals were progressively exterminated by man as he moved through the Central American area. In this regard it is interesting to note that today only one large mammal, Odocoileus, is to be found in the nonforested tracts along the entire Pacific drainage from Mexico to South America whereas Tapirus and two species of brocket deer (Mazama) occur in the forested tract over the same distance.

Archaic Stage. (Willey and Phillips, 1962). The oldest dated site thus far reported upon in Panama (Cerro Mangote; McGimsey, 1956) is a little over 6,000 BP (Baudez, 1963). Baudez summarizes the culture at Cerro Mangote thus, "The community pattern is of the semi-permanent sedentary type. The food sources consist of shellfish and game, no evidence for agriculture having been found." The next known site in this sequence is located near the Parita river in Herrera Province not far from the ocean and is termed the Monagrillo site (Willey and McGimsey, 1954). This is the earliest ceramic site thus far located in Panama and is one of the oldest ceramic sites in Latin America - 2,130 BC (Lothrop, 1959).

At the Mongarillo site no evidence of agriculture was discovered

(But see chapter 3). Chipped stone projectile points and scrapers were found as well as pebble choppers, pestles, grinders, hammers, anvils, and grinding stones. The two authors (Willey and McGimsey) hypothesize that the earliest phase of the Monagrillo culture was "apparently based on a shellfish economy. Sixty two molluscan taxa were described from the site of which Ostrea chilensis and Tivela gracilor" occur in much greater abundance than the others and they may be considered the staple shellfish of the people living at the site." Vertebrate remains identified included Odocoileus virginiana ssp. "undoubtedly the major mammalian staple of the ancient inhabitants," Tayassu pecari, Procyon sp., Grampus rectippina (I have changed some of the names to bring them into line with the usual current usage); some other unidentified cetacean material; 3 unidentified rodent skulls; some unidentified avian humeri; 62 plastrons assigned to Podocnemis expansa; 5 plastrons assigned to Amydidae; 37 fish vertebrae; 50 dactyls from a crab, Menippe frontalis; two barnacles, Tetraclita; an unidentified collection of 105 animal remains.

The assertion that the earliest phase of Monagrillo culture was based on shellfish is open to question. Such a conclusion is derived from a belief that the relative quantities of each taxon recovered from a midden is correlated with the relative importance played by each taxon in the diets of the people previously occupying the site. However, consideration should be given to the following questions:

Did the people discard all or almost all their trash on one site? The extremely low incidence of rodent material in the midden seems to be misleading - the following rodent genera must have been available locally, Proechemys, Agouti, Dasyprocta. Especially the spiny rat,

Proechemys, may well have been abundant and this fairly large rodent (body length 6-12 inches) is quite edible and easily trapped. No lagomorph material was described but Sylvilagus must have been present and in fairly large numbers; no iguana (Iguana) remains were described but this large, common and very edible lizard must surely have formed part of the diet - especially during the dry season when gravid females are easy to catch and with their eggs provide an extra source of protein. A most important lack in the site remains is vegetable material. The grinding stones indicate, however, that plant food must have figured significantly in the diet. It seems reasonable to assign to plant food a preminent place in the diet of these people. Even in cases where hunting is developed to a much higher degree than seems to have been the case at Monagrillo there is often a heavy dependence upon plant food. A basic problem relates to the relative durability of various substances of plant and animal origin after they have been cast casually upon the surface of the ground and thence subjected to the attack of insects, fungus, bacteria, carrion feeders, and the heat and humidity of an A climate for over 6,000 years. The wonder is that any animal remains were found. There is the possibility the site was only seasonally occupied - perhaps during the dry season - and that wet season sites exist elsewhere. Another objection to the statement regarding the importance of shell fish is that it is questionable that the resource could have sustained year around exploitation. In the present day when the gathering of Ostrea is done as a minor activity of the local campesinos it is clearly evident that even these efforts tend to quickly deplete the resource so that periodic cessation of the activity if necessary for recovery of the shell beds to population levels great enough to justify further exploitive effort.

## Human Population and Distributions (Paleo-Indian through Archaic)

Of basic importance to an attempt to relate the activities of human groups to biotic change is the establishing of human population numbers and distributions. However, before such a task can be attempted it is necessary to know something about the carrying capacity of the exploited biotopes in relation to the technological levels of the people being investigated. Alas, for Panama this is all but impossible to accomplish for peoples at the pre-agricultural level. To assist in deriving a gross approximation of the possible densities of human populations on the isthmus of Panama in those early days the demographic data of Steward and Faron for South America and Central America (1959) may be employed. These authors have assigned to hunters and gatherers in South America arithmetic population densities which range from 0.2 person /$m^2$ to 1.1 persons /$m^2$.

If an arithmetic population density of 0.2 person /$m^2$ prevailed in Panama throughout most of the pre-agricultural period there would never have many more than 6,000 human inhabitants in the area at any one time. However, it may be assumed that the larger figure of 1.1 persons /$m^2$ can be applied to Panama since the cited authors assign the value to comparable (?) cultural situations where the ecological base is no greater than we may presume Panama's to have been. This will produce a maximum human population of approximately 33,000.

If the hypothetical population of 33,000 people is restricted to the areas which were exploited, i.e., if we attempt to achieve a measure of the physiologic population density, we may suggest that the focus of exploitive activities tended to concentrate the people within a belt running parallel to the coasts. Let this belt average ten miles

in width (greater in some places much less in others) and by using an estimated one thousand miles of coast line we can then estimate a crude physiologic density of 3.3 persons/$m^2$. If it be kept in mind that the Pacific side may have offered greater opportunities for pre-agricultural peoples than did the Atlantic side then we might increase the density to 5.0 persons/ exploited $mile^2$ on the Pacific side and reduced the Atlantic belt density to 1.6 persons/$m^2$. Although further (hypothetical) refinements are possible they are not justified by the presently available data. The purpose of this highly tentative reconstruction has been to suggest where the exploitive activities were greatest in order to get at the fundamental question as to what effects the exploitation may have produced on the biological patterns on the isthmus. May 5 represents an attempt to reconstruct the human population density patterns on the isthmus during this period before the appearance of agriculture. No allowance is made for a growth trend over the considerable time period involved. The maximum population may have occurred just prior to the advent of agriculture or may have been reached long before and then fluctuated in the manner to be expected of any mammal whose numbers are largely dependent upon a variable wild food supply.

## Phytophysiognomic Changes
## (Paleo-Indian and Archaic)

The attempt to reconstruct the population levels of pre-agricultural peoples on the isthmus did not lead to the establishment of particularly large density values even when the populations were ecologically restricted to particular parts of the isthmus. However, it should be kept in mind that a very considerable time depth is

involved, perhaps more than 15,000 years, and thus the cumulative biotic pressures of even small human populations may result in significant alterations. If one can correctly assume that all the cultures present at any time on the isthmus possessed a knowledge of fire making one is faced with the need to accept the view that millenia-long burning of vegetative cover must have produced some profound effects on regional phytophysiognomy. It is well known that fire was used as a hunting tool much farther back in pre-history than we are here considering and it was very likely an important tool of the early cultures which drifted across the isthmus. Because of the coastal (regional) differences of climate on the isthmus (see Chapter I), it is certain that fire was most effective as a tool for hunting and thus as a factor of vegetational change on the Pacific side - particularly in the areas which today (but not necessarily in the past) have an Aw climate. In these areas fires are still set each year during a period of up to four months. (The subject of burning has been receiving increasing attention, see, for example, Budowski, 1956, Bartlett, 1955, 1956, 1957, Cumberland, 1963, Johannessen, 1963, Stewart, 1957, Sauer, 1958.)

Of significance are the present-day concentrations of certain woody plants which are fire resistant. The following taxa seem to be the most abundant and widely distributed of such plants in Panama (and Central America) Curatella, Byrsonima, and Anacardium excelsum - "chumico" nance" and "maranon", respectively. (Maranon is also known in the U.S. as cashew.) Curatella is so intimately associated with burns that this writer has found it to be an excellent indicator of past fire in a given situation when the plant is present. Nance and maranon withstand droughty conditions and fire quite as well as

chumico.

That the shrub and grass "savanna" areas of Panama are not particularly old is indicated by a lack in such areas of a distinctive fauna. Writers have noted the paucity of mammals and attention has been drawn to the lack of a special stingless bee (Meliponidae) fauna or special termite (Isoptera) fauna which suggests a recent time of origin of the so-called savanna areas (Michener, 1954; Emerson, 1952). In Chapter I a brief description of the present phytophysiognomic aspects of Panama was given and the accompanying map shows the present general pattern of vegetation in the country. It is impossible to point to any part of the country and say that the present conditions may be directly related to the cultural activities of people belonging to the pre-agricultural sequence. On the other hand, if the suggestions presented above are followed as to where the exploitive activities and population densities may have been greatest it appears that vegetational changes on the Pacific side of Panama were of greatest importance. It may be that some of the most anciently disturbed locales are now a part of the marine environment-they having been drowned by eustatic changes in sea level in post-Pleistocene time. The Cocle Plain may have been the most seriously effected area now available for observation but the obvious ecological disturbances in that area can only be said to have been initiated in the pre-agricultural period and, as will be demonstrated below, further developed and intensified later. It is here suggested that long before the advent of agriculture, however, fire and men had seriously altered most of the Pacific corridor from Mexico south to and perhaps into South America. On the other hand, it is suggested that only minor disturbances were accomplished by human agency in Atlantic and montane forests.

## Zoogeographical Effects

Perhaps the major problem confronting an attempt to reconstruct the zoogeographical past on the isthmus is that there is no agreement as to the time available for the various faunal dispersals and other events to have taken place. In this discussion and some of those to follow an attempt is made to isolate the animal (chiefly mammalian) taxa which, on the basis of available information, appear to have been present on and/or dispersed across the isthmus in late Pleistocene and/or Recent time, i.e., within the time span which seems to encompass the total period during which man has been in the area. Of prime consideration to such a determination is the taxonomic status of each implicated mammalian taxon in South America and the extent of the areal dispersal into South America.

There is little agreement at present as to the expected rates of mammalian subspeciation and speciation. Mayr (1963) masterfully reviews this problem and shows that virtually each taxon in each situation must be treated as a separate case. He notes that the European rabbit has become subspecifically distinct within 500 years in certain areas to which it has been introduced and indicates even more rapid rates for other taxa.

As a working guide this writer has pursued the following course: if the available geological evidence indicates a late Pleistocene or Recent entrance of the mammalian taxon into South America; if the taxon is found chiefly in non-forested situations; if the taxon has not yet penetrated any great distance into South America but because of its known ecology may be supposed to do so in the future whenever an opportunity occurs; and if the taxon is only subspecifically different from its more northern congeners, the writer has proceeded with the

hypothesis that such a mammalian taxon comes within the per-view of any discussion wherein an attempt is made to evaluate the human cultural element as a factor in animal dispersal across the Isthmus of Panama into South America.

If it be kept in mind that the fire caused phytophysognomic changes indicated for parts of Pacific Panama also occurred in most of the Pacific-side area to the north of Panama on into Mexico, it is tempting to suggest that, long before the advent of agriculture, man had opened a continuous corridor into South America composed of shrubs, second growth woodland and varying amounts of grass. Through such a corridor a number of animal taxa could have moved north and south. On the other hand, a number of difficulties to such a hypothesis are present and must be considered.

One important difficulty is that today the corridor is not continuous but is interrupted at several points by enclaves of forest, the most important of which is in southwestern Costa Rica in the Golfo Dulce region. However, all of the forest complexes in the Golfo Dulce area are seasonal to some degree and located adjacent to them are "savannas" whose phytophysiognomic and floristic characters are essentially the duplicate of those described above for Panama. It would not have required any exceptional effort for early people to have disturbed some of the dryer forest formations but pre-agricultural people would not likely have had reason for clearing the heavy monsoon-type forest of the Golfo Dulce area. On the other hand, it has been suggested in Chapter I that there is reason to suppose that climatic conditions on the entire Central American Isthmus were different during the latter part of the Pleistocene (Wisconsin) than they are at present. If such changes included a greater tendency toward a dry season than is presently the case then the resulting dryer forest formations (or woodland) would have been more easily degraded by fire.

Certain faunal phenomena suggest that some kind of "savanna" corridor has in fact existed at some time or times in the past. The questions are: did such a corridor come into being before human arrival and thus have no bearing on human activity or did man, as has been suggested here, open the corridor.

To partially illustrate the problem, the cottontail, Sylvilagus floridanus, has the following general geographical distribution at present: widespread in North America (chiefly the USA) and south as far as the woodland - grass "savanna" areas of Guanacaste Province of northwestern Costa Rica. Thence a major break in the distribution until the species again appears in coastal (Atlantic) areas of Colombia and Venezuela, the arid scrub-lands of the upper Rio Magdelena Valley, the upper Rio Orinoco area and on the islands of Los Testigos and Margareta in Venezuela (Hershkovitz, 1950). Hershkovitz, (1950) who has made field observations on these lagomorphs in South America has the following significant comments regarding their choice of habitat:"

> The species (S. floridanus) is never found in virgin or fully established forests. Cottontails could have been introduced by man or could have entered the continent from Central America by following the interconnecting maze of natural and artificially created savannas in Panama and northwestern Colombia. These savannas may have been more numerous and more extensive than is indicated at the present time.
>
> Primary forests are natural barriers to the spread of cottontails in South America. Thus, the northern Colombian cottontail (S. floridanus supercilliaris) is abundant along the base and cleared

> foothills of the Sierra Nevada de Santa Marta but is absent from savannas in the Sierra Nevada at 1,000 meters and more above sea level. These montane savannas, apparently affording ideal habitats for cottontails, are separated from lowland savannas by a continuous belt of forest. On the other hand, the same cottontail has penetrated clearings on the opposing slope of the Sierra de Perija to as high as 1,000 meters above sea level where these clearings are continuous with those of the lowland.

Hershkovitz further suggests that the insular forms noted above must have been introduced to the islands by man.

Putting aside, for the moment, the possibility that man may have physically transported the cottontail to South America and focusing on the question of man-aided terrestrial dispersal we come up against the fact that the cottontail is not known from "savanna" habitats in Panama - In fact the animal has never been recorded from Panama - even though apparently suitable habitats exist for it there. There is the chance that collectors have merely missed it but this seems doubtful. The Chiriqui' area, for example, has been collected in by careful field men and the only lagomorph discovered there is S. brasiliensis, a South American Tapiti. The same species has been taken from near Panama City, the Canal Zone, eastern Panama, Isla del Rey, and there is a sight record from the northwestern corner of the Azuero Peninsula. This writer has also seen this mammal at various points in Herrera Province and Coclé Province.

It is important to note that S. brasiliensis occupies many situations in Panama which would seem to be well suited to its (nearctic ?) congener, that is, brush, second growth scrub and grassy areas as well as heavily forested sites which are not available to S. floridanus. It would appear that perhaps the tapiti is a better competitor but Hershkovitz has indicated just the opposite for Colombia saying that the cottontail here replaces the tapitis in artificial savannas and considers the cottontail to be the more aggressive animal.

An examination of the range of the cottontail in Central America may assist in partly resolving the problem. Presently available information indicates that the cottontail occupies BSh (hot steppe climate) and Aw climatic areas in Mexico and Central America and is absent from Am and Af situations. Furthermore, it appears that only the dryer portions of the Aw climate contain cottontails. In Colombia the animal occupies what appears to be the same kinds of climatic areas. It may, therefore, be suggested that most of the present Aw climatic areas of Panama are too moist for the animal. It may then be further suggested that dryer Aw conditions once prevailed in Panama and southern Costa Rica and the animals followed the corridor, but later slightly more humid conditions developed which did not permit the animal to survive in Panama. The logic of this seems to conform with the present disjunct distribution of this lagomorph in the southern part of its range in Central America. Does this rule out any possibility that human agency played a role in its dispersal? Not necessarily. If dryer Aw (and perhaps BSh?) conditions once occurred on the Pacific side of the Central American isthmus in a much more extensive pattern than at present there may have remained tracts of deciduous forests to block completion of a continuous corridor and those forests might have been disturbed by escaped fires during the

dryer periods of the year thus opening, at times, dispersal routes. In partial support of this suggestion is the limited amount of time which seems to be available for this dispersal. Cottontails seem to have arrived very recently in South America and differ only in subspecific characters from their more northern congeners. Furthermore, their penetration thus far into South America is restricted to a very small part of the north end of the continent in spite of the aggressive character asc. ibed to the species by Hershkovitz.

It has been suggested above that the absence of cottontails in Panama might be the result of changed climatic conditions which have occurred since the animals dispersed across the isthmus. There is also the possibility that the species was extirpated in Panama by man. This possibility seems quite remote, however, if it be kept in mind that the animal has a high reproductive rate and has resisted extremely heavy human predation pressures in other parts of its range for very long time periods.

Hershkovitz has suggested that the animal may have been transported to South America by man. This is a very distinct possibility if only the known habits of aborigines are taken into consideration. However, such a transport would almost certainly have involved the employment of sea-going craft which appear not to have been a part of the cultures under discussion. This possibility would be most appropriately taken up in the next chapter but can be dismissed here by taking note of the fact that if the nearest the cottontails ever came to South America is in their present area of distribution in Costa Rica it would have been necessary tocarry live hares <u>across</u> Costa Rica to the Atlantic, put them into boats, and after a voyage of considerable time, put them ashore in northern Colombia in a live condition. The writer can only conceive of such transport as being all but impossible. There is no reason why cottontails would have figured

as a trade item. It seems that a terrestrial dispersal is indicated, whatever the human influence may or may not have been.

The foregoing discussion has focused on one mammalian taxon for the sake of conveniently offering what seem to be the principal elements to be considered in evaluating the possible importance of early man as a factor in the dispersal of animals across the isthmus. Obviously all suspected taxa must be considered for the full discussion. However, insofar as man-aided dispersals at this pre-agricultural level are concerned there seems little to be gained in continuing what is of necessity a very conjectural discussion. Briefly, it may be indicated that other mammalian taxa would figure in a more lengthly conjectural statement, e.g., white tail deer, Odocoileus virginiana; gray fox, Urocyon cinereoargenteus; raccoon, Procyon lotor; spotted skunk, Spilogale sp., hog nose skunk, Conepatus sp.

An even more difficult element to evaluate is the possible selective effect that human predation may have had upon all exploited animal taxa. That such exploitation does indeed have evolutionary implications has been noted. (Mayr, 1963). Three particular aspects of the problem may be mentioned, viz., the effects of reducing the size of the gene pool of individual populations, the implications associated with the removal of "natural" barriers between allopatric species resulting in sympatry, and geographically isolating into separate small populations that which was formerly one population. All of these probably occurred in the area under discussion. But what the details were are unknown at present. One does wonder, however, if the present large array of mammalian subspecies on the isthmus is only a part of the widely remarked but little understood tropical taxonomic proliferation or if it is in some way related to human factors. It appears that the question of human actions as a factor

influencing selection in wild animal populations has not received much attention for any part of the world. Mayr (1963) has summarized most of the available data relating to these fundamental questions.

# CHAPTER 3

## ABORIGINAL AGRICULTURALISTS

Introduction. It is not yet possible to assign a date to the period when people with agriculture were first present in Panama. This difficulty is due in part to the continuing reevaluation of presently available archaeological materials. Thus it might be asserted that the earliest date for agriculture in Panama is approximately 230 ± 60 BC (de Vries, 1958). This would be based on a site in extreme southeastern Chiriqui Province (Lathrop, 1959). The economy attributed to the people once occupying the site was summarized (Baudez, 1963) as follows: agriculture was probably the main source of food, but fishing and hunting remain (ed) important. In Chapter 2 it was noted that the Monagrillo site did not yield evidence of agriculture. On the other hand, on the basis of renewed evaluation of the same data, Willey (1960) has suggested the possibility that "incipient cultivation" may date back to as much as 4,000 years BC in Panama and that "village farming" with maize (Zea) as a basic crop may have been present in Panama as early as 1,500 BC.

Since any attempt to reconstruct man-biotic relations at this period of prehistory in Panama is conjectural, the oldest dates suggested above will be followed as a guideline in the discussions to follow. This results in a considerable overlap of the discussion in the previous chapter but cannot be avoided. It should be pointed out that the more ancient agriculture proves to be on the Isthmus and in contiguous areas the greater is the probable importance of man as a factor in biotic disturbance in the region.

Archaelogical sites dated as more recent than the ones mentioned above seem to indicate a gradual shift from incipient agriculture to village agriculture with an accompanying trend upward in human population numbers and densities. If the earliest date above for agriculture are provisionally accepted there is a time period available of almost 5,500 years prior to the first European contact on the isthmus. The nature and scope of agricultural activities were of course not constant through this period but they were of major importance at the time of first European contact.

The "incipient cultivation" stage as used by Willey (1962) may represent the starting point of plant cultivation but very little is known about the working features of this stage. There have been published studies of contemporary cultures which seem to be at the same stage of agriculture but of course it is possible that the techniques of such people are only similar in a general fashion to those prevailing several millenia in the past. Yet it must also be realized that primitive cultivation is at best limited in scope and technique and it is acceptable to draw inferences from the contemporary situations just mentioned.

One of the more important of such studies is by Leeds (1961) and it deals with incipient tropical forest horticulture among the Yoruro, a culture group occupying, at present or in the recent past, a portion of the Venezuelan llanos at a distance of 450 to 600 miles inland from the Atlantic coast. The people's food-providing technology includes hunting, gathering, fishing, animal husbandry and horticulture. The basic cultivation techniques are those of shifting cultivators in general (shifting cultivation has many synonyms such as milpa, ladang, swiddening, slash and burn, fang, chitemene, and so on, including what seem to be purely anthrological

designations in some instances). The essential features to which attention is directed here is the employment of tree felling and the later burning of downed-material to make way for planting and then the periodic abandonment of cultivated plots due to factors such as soil exhaustion, grass encroachment, or super-natural beliefs (see Canneiro, 1956, for a discussion of some of these factors). It seems that the just-named elements must come right at the beginning of agriculture and therefore the important changes that take place subsequently are related to slow improvements of the basic techniques of cultivation and development of improved crop plants as well as improvements in harvesting and storage techniques. Although we are here principally concerned with those activities which are directly involved with land use, improvement in the total technology is related to greater carrying capacities and thus to larger population densities.

Although it is not stated in so many words, one does get the impression from some of the archaeological literature that agriculture in Panama first appeared in the western region, that is, in the areas which have thus far received the attention of archaeologists. Wheter or not the impression is correct this writer suggests that more optimal conditions may have existed elsewhere, as for example, in the eastern part of Panama. As was pointed out in an earlier chapter, there is almost no hard information about the climatic conditions that existed on the isthmus during the time now being considered but it might be argued that even allowing for some change the present Aw area in the west must have been less well favored for shifting cultivation techniques than would the more forested conditions of the present Am areas of eastern Panama. A major problem is that the archaeology of Darien is very poorly known. With the exception of a brief and peripheral reconnaissance over thirty years ago

(Linne, 1929) and an even more modest effort in the last decade (Cruzen, 1959) essentially nothing is known of Darien's pre-history. It is to be hoped that this will not remain true for very much longer.

## SPANISH CONTACT

Human Population, c. 1500 A.D. Although at present much of the lowland of Darien is very sparsely populated by man this was not the case at the time of the first European contact in the beginning of the sixteenth century. Moreover, the Atlantic littoral which today is very sparsely populated along much of its length, particularly in the eastern part, was well settled at the time of Spanish entry. The contact period documents attest to large and at times dense human agricultural populations in areas which today are largely despoblado.

Published estimates of the number of Amerinds present in Panama circa 1500 A.D. vary widely and reflect the essential lack of hard demographic data.

Rosenblatt (1945) preferred to attempt an estimate for all of Central America which he gave as 800,000 inhabitants, a figure which most certainly is far too conservative. He did cite a general source (Alba, 1935) in which an estimate for Panama alone was given as 800,000 but no substantiation is offered.

Guzman (1956) estimated a total of 400,000 persons for the territory of present-day Panama. He considered population densities to have been greatest in western Panama because of accounts that indicated more fighting men present there than in Darien.

Steward and Faron (1959) offered an estimated aboriginal population in Panama of 225,000 but this does not seem to agree with a map in the

same publication in which the population density is given - for the same time - as 4.8 persons/mile. A population of 225,000 would yield an arithmetic density of approximately 7.5 persons per square mile. One of the co-authors of the just cited work earlier (1949) estimated a total aboriginal population at contact of 224,600 (the more recent figure apparently being "rounded" from this) of which 150,000 were placed in eastern Panama, 74,600 in western Panama, and with arithmetic densities of approximately 7.8 persons per square mile and 5.2 persons per square mile respectively. Steward also indicated that community size was highly variable and may have ranged between 500 to 3,000 inhabitants each.

The most ambitious recent estimate is that by Fuson (1958) who reviews the literature and concludes that there were possibly a million inhabitants of which one-half may have been located in the plains of central western Panama.

Obviously, this is a numbers game at which many can play and each with the same excellent chance for failure. Nevertheless, it is necessary to adopt some tentative figure here if the discussion is to proceed.

I think that Fuson's estimate errs heavily on the side of too many people since it yields a gross arithmetic density of approximately 30 persons per square mile which appears quite at variance with what is known of carrying capacities of similar habitats inhabited by people at a similar economic level. Since no one, including this writer, would suggest that all of the territory was equally settled one must accept densities exceeding 50 or 60 persons per square mile of expolited area - a figure that is not acceptable.

For the purposes of this investigation, the greater number of people that can be postulated, the greater is the possibility of inferring major ecological impact. For this reason as well as for considerations of

what seems to be approximately correct ecologically the conservative estimates of Steward (1949) will be followed.

Guzman (1956) estimated that 80 per cent of the land area of Panama lies below the 800 meter (2600 feet) contour and if it be assumed that this represents all usuable and used land circa 1500 A. D. then one may derive a crude physiologic density for the human population of approximately 9.6 persons per square mile (using a total population of 224,600 and 80 per cent of a total land area of 28,576 square miles). Then, to go a step farther, if the regional distributions of Steward are followed, a physiologic density of 14 persons per square mile may be derived for eastern Panama (using an area of 13,425 square miles) and a physiologic density of approximately 6 persons per square mile is derived for the western part of the country.

Further refinement seems possible. In eastern Panama the greatest human population densities were apparently aligned with rivers and exploitation must have decreased with distance away from these ecological foci. Thus, it may be suggested that several distinct bands of physiologic population densities existed in eastern Panama. Similarly, in western Panama there were, as there are today, important habitat variations, which must have produced varying degrees of population densities. These estimates are presented in Map 6. Examination of the map will show that the distributions have been determined on the bases of ecological conditions and economic levels as well as data from contact reports although the last have been used sparingly. It should be particularly noted that a continuous strip of occupied territory is postulated for the Atlantic littoral and a continuous belt of occupied territory is also indicated for the Pacific side although the latter is much more varied ecologically

than is the former. Only the higher elevations probably escaped the attention of these farming people.

Vegetation at Spanish Contact. Contemporary accounts in the early sixteenth century clearly indicate the fact that vegetation alteration was of a large scale. The first of such accounts is by Ferdinand Columbus (Iglesia, ed., ((1947))) which follows (C.F.B. trans.):

> Without further delay, the Admiral continued navigating until he entered Porto Belo, to which he gave this name because it is very large, attractive, and well populated and it is possessed round about with much cultivated land...The region which surrounds the port is not wild but is cultivated and filled with houses distant a rock or ballesta throw from one another: it appears like a painted object, the loveliest that had been seen.

Leaving the haven of Porto Belo, the Admiral sailed on to the east and put in near Nombre de Dios:

> ...and because all those environs and islets were filled with maize fields there was given them the name Puerto de Bastimentos.

Turning about and sailing west over the previous course the group put in at the Rio Belen (see Map 6) and mention is made that in a near-by area there were:

> ...six leagues of maize fields, which are like fields of wheat.

The early chroniclers supply elusive and often geographically vague information for Darien. One of the important of the writers of this period, Andagoya, (In Cuervo, 2, 1982), spoke of the area in the following manner (C.F.B. trans.), "the first province to the west of Acla

(A then Spanish base which was located not very far westward on the Atlantic coast from the present Panama - Colombia border) is Comogre where populated lands and savannas begin: from that area it was well populated." When speaking of settlements in the area Andagoya vaguely refers to "these provinces" and does not specifically state which area of total Amerind (probably all Cuna-Cueva as is usually assumed in literature) territory he is referring to. He indicated that "In these provinces there are no large settlements, but each settlement has three or four or more houses ...each one located adjacent to the owner's cultivated land."

Drawing attention to Andagoya's remark that savannas began at Comogre, Romoli (1953) in her able book treating the sixteenth century in eastern Panama, placed Comogre in the upper Rio Bayano region and adjacent lands throughout the entire Bayano lowland. (Savanna ((or sabana)) in many of the early documents appears to have been a word acquired by the Spanish on the islands of Hispaniola and referred to open country with grass and trees ((see Johannessen, 1963 for a partial discussion of this subject))). There appears to be no reason why similar conditions did not occur in the Chucunaque - Tuira valleys as well - since they were also populated with the same or similar people.

That usually reliable chronicler, Oviedo, presented, in his account of Balboa's passage across the isthmus to the "discovery" of the Pacific Ocean, a picture of at least partially open country and indicated that the major s ttlements, at least, were connected by broad trail s ("Caminos") - a feature still remaining in the Cuna area at present. Because so little mention is made in Oviedo's account of cutting paths one deduces that

the land must have been relatively open. No mention is made of encountering difficulty in maintaining direction - a major problem where forest cover is present. It is also significant that the last leg of Balboa's journey to the Pacific shore was overland whereas today it would be much faster and easier to make the trip down the Rio Chucunaque to tidewater. (See Oviedo, 1944, edition, tomo7).

The surviving documents written by Balboa (see Altolaguirre y Duvale, 1914, for these materials) provide very little information beyond the well known interest of the Spaniards in gold. On the other hand, the virtual lack of attention given to the physical milieu by Balboa strongly suggests that the country over which he and his group passed was in major part far more open than is the case today.

Having placed eastern Panama in their control, the Spaniards soon directed their attention to western Panama south of the central sierra. In 1516 an expedition led by Gaspar de Espinosa set out and passed through Comogre and westward to Nata in the Cocle Plain (Espinosa, ((1982))). All of the land over which this agent of the Spanish Crown passed was described by him as "land as flat as the palm of the hand, a very healthful land and all in savannas without forests other than trees which are on the banks of the rivers, and it is (also thus) in the land from Nata to Guarari... (on Romoli's map, Guarari is shown as a part of the eastern region of present-day Los Santos Province). In all this land in summer or winter it is possible to go on horseback as well as or better than in Castile (and) this through all that has been discovered as (well as) that which is possible to see on ahead." (C.F.B. trans.) I believe Espinosa's route led down the Rio Bayano valley to the coast and thence westward since this agrees best with the placement of Comogre, the starting point.

Wherever the Spaniards penetrated in the west to and well beyond the present Costa Rica-Panama border, they encountered large Amerind populations. As the contemporary accounts give no evidence of forests the conclusion to be drawn in obvious, viz., that all or most of western Panama, in the lower areas particularly, were open savanna lands. (See Map 7 for a hypothetical vegetation distribution c. 1500 A.D.)

## SOME ZOOGEOGRAPHIC IMPLICATIONS

Mammalian Dispersals. If 5,500 years of agricultural activity prior to Spanish contact areavailable there would appear to be sufficient time to have made possible the dispersal of some mammals across man-removed forest barriers into South America. If the time available for pre-Columbian agriculture in the Panama area is only 1,800 years, the possibilities of such agriculturally associated dispersals must be considerably reduced although not entirely removed.

The mammalian taxa which appear to have been the most likely candidates for such dispersals, if they occurred during the pre-contact agricultural period, would be those mentioned in the previous chapter, viz., cottontails, Sylvilagus floridanus, whitetail deer, Odocoileus virginiana, grey fox, Urocyon cinereoargenteus. All three of these mammals seem to take rapid advantage of comditions when they are altered to fit their ecological requirements. This is especially true of whitetail deer and this taxon may have dispersed even if only the briefer time given above was available. Goldman(1920) indicated that this deer probably followed the disturbed area caused by railroad construction across the Isthmus in the midppart of the 19th century. In the United States experience has shown that the animal responds very fast in numbers when habitat changes take place. During the agricultural period a continuous corridor of

disturbed second-growth vegetation probably was available West to East across Panama and probably into South America (see Map 7). Similar disturbed conditions must also have obtained in Central America (as remains the case in most of the Central American area today.)

That whitetail deer populations were high in parts of Panama in the early sixteenth century is attested to in the documents of the period. Espinosa (op.cit.) remarked on the great stores of deer meat available in Indian villages in western Panama and Andagoya (op.cit.) related the technique of using fire to hunt deer and further indicated the importance of this mammal to aboriginal hunters. The land-use techniques of shifting cultivators produce optimal second-growth vegetation conditions which greatly benefit this animal's populations. Lack of fire-arms apparently prevented over exploitation. It would be very important to know if these deer were present in disturbed areas on the Atlantic side of the isthmus and in eastern Panama during these times. Except for the dispersal of deer along the railroad route it has long been held that Odocoileus does not occur in these areas at present. However, this taxon has been reported in the banana lands of Bocas del Toro (Gordon, 1961) and Dr. Pedro Galindo informed this writer that the deer was recently discovered in eastern Darien in an area of former important Indian settlement.

As indicated in the last chapter, the cottontail, Sylvilagus floridanus is not now known from Panama and no very recent record of the grey fox is available.

Avian Dispersals. Volant animals pose special problems in terms of their dispersal potential but some taxa do appear to be candidates for human-assisted dispersals across the isthmus. The avian family probably most responsive to the creation of open lands and/or scrub and second

growth is finches, fringillidae. Some of the taxa which might have figured in such dispersal include the Ruddy-Breasted Seedeater, Sporophila minuta minuta, the Variable Seedeater, Sporophila aurita aurita, and the Thick-billed Seed Finch, Oryzoborus funereus. All of these are birds which keep to open country or low scrublands. In Panama, Central America and South America they do not seem to occur in forests. The Green-back Sparrow, Arremonops conirostris, may also have thus dispersed into South America but it may have moved through beach-edge vegetation (see Wetmore, 1957, for discussion of habitat on Isla Coiba.)

Reptilian Dispersals. The herpeto-geography of Panama and adjacent areas is very imperfectly known and it is extremely difficult to infer what the effects of vegetation alteration by man may have been on reptile and amphibians. Dr. Harold Heatwole has kindly permitted this writer to quote from a paper which he will soon publish (Heatwole and Sexton, in press). The authors have indicated that a common lizard in parts of Panama, Ameiva ameiva ss which frequents non-forested habitats, may have once had a continuous distribution from Panama into South America but the present forests of Darien now cause a disjunct distributional pattern. The authors suggest that the texon arrived in Panama from South America during the upper Pliocene, thus following a suggestion by Duellman (1958) that a continuous savanna belt joined South America to North America during the upper Pliocene and probably, according to Duellman, into the Pleistocene. Without here examining Duellman's conclusions vis a vis Isthmian paleoclimatology, it would seem that there are some difficult problems in regard to time and speciation. If, as has been suggested, the Ameiva ameiva populations of Panama are assignable to the same subspecies as the South American forms, praesignis, it is necessary

to accept that there was no significant separation of these populations for over a million years with man arriving in time to hold open the corridor through vegetation removal until the 16th century A.D. when abandonment of the area of eastern Panama led to a closing of the million year old corridor and the geographic separation of the subspecies.

An alternative hypothesis might be that the taxon here being considered dispersed for the first time into Panama during the period of human occupance of Darien after there had occurred sufficient change of conditions to make such a dispersal possible. Heatwole and Sexton indicate that the lizard follows closely on open areas created by man and is particularly well adapted to maize fields. Part of my argument hinges upon an assumed rate of genetic variation of separated gene pools. But if the Panamanian and South American populations of this species of Ameiva are identical it would appear that a fairly recent entry into Panama is indicated. A million years of continuous distribution would seem to have led to clines so that now at least two very distinct subspecies would be recognized from the geographic ends of the present total range.

Transport of Animals. The possibility that some animal taxa were transported by man within or into Panama must be considered.

During the agricultural period the means available for such transport were probably by no means modest. It is well established that trade was carried on by boat over ocean waters and for considerable distances along both coasts of Central America (for a partial review of the aboriginal employment of boats see Driver and Massey, 1957). Transport by human labor was also important in the area, perhaps even to a greater degree than were boats.

Of particular interest to the question of transport of mammals into Panama is the presence of squirrel monkeys, Saimiri oerstedi, in extreme southwestern Panama and in adjacent parts of Costa Rica. This very social primate occupies, in Panama and Costa Rica, very disturbed situations. It is not found in forests but in shrub or highly deciduous woodlands and is particularly abundant in banana plantations.

The nearest living congeners occur many miles to the south in the Amazon basin (not having, as Goodwin, 1946, indicated, a continuous distribution from Panama into South America). Cabrera's remarks (1957) in regard to the taxonomic status of the Central American Saimiri are as follows: (C.F.B. trans.)

> The numerous "species" which have been described for this genus should be reduced to two at the most: sciureus of South America and oerstedi of Central America. And it is even probable that the latter is not a (separate) species but is a subspecies of the former. The authors have given excessive importance to purely individual differences...

If the Central American Saimiri is but a subspecific form of the South American species, transport and later liberation seems possible. Why such a transport took place, if it did, can only be conjectured. It is well known, however, that tropical Amerind cultivators are excessively fond of keeping wild animals as pets. For this reason this little primate, a great favorite in the Amazon basin among Amerinds, might have been traded. Movement of animals in pre-Columbian time is well accepted (see, for example, Westermann, 1953).

There do not appear to be any important barriers to the spread of this primate into many habitats in Panama and Costa Rica (excepting recent

removal of all shrub cover for pasturage and persecution by local hunters). The post-Columbian maximum distribution may have represented the extent of dispersal from a single point of introduction in western Panama. Its present distribution is much less now than it was only a few years ago when it was common on the lower slopes of el Baru (see Bangs, 1902) but it is not now present there and in fact is now only to be found on some of the islands just to the south of David (Chiriqui Province) and in the banana lands a little to the west (in Panama). The disturbed conditions of vegetation which were so long a part of the ecology of the pre-historic period of Panama would seem to have favored the much greater dispersal of this primate than seems to have been the case. Perhaps this can be answered by an introduction in the late pre-Columbian period?

Certain Panamanian insular occurrences of mammals suggest the possibility of transport by man. Of particular interest is the (known) mammalian assemblage on Isla Coiba. Excluding Chiroptera, the mammalian taxa are: Coiba opossum, Didelphis marsupialis battyi; Coiba Howler Monkey, Alouatta villosa coibensis; Coiba Agouti, Dasyprocta coibae (surely an insular race of punctata?); White face Monkey, Cebus capucinus. Rothschild's Whitetail Deer, Odocoileus virginiana rothschildi. Thomas (1903) in commenting on this sparce assembly rather incredibly suggested the following by way of explanation:

> Probably at some period in its history the Island was lowered to such an extent as to drown out all burrowing and terrestrial animals, while leaving such species as either were arboreal (Monkeys and Opossum) or were able to live in some slight depth of water or swampy soil (Odocoileus and Dasyprocta).

Additional collecting of mammals on Coiba will most certainly extend the list, especially insofar as chiropterans are concerned, but giving

all due allowance for what may have been casual collecting of Coiba's mammals in the past, the list is peculiarly short.

It is interesting to note that every mammalian taxon on the list just given is considered to be quite acceptable human food and certainly these taxa were important aboriginal food items. Could it have occurred that in pre-Columbian times these animals were transported to Coiba by man and there released to provide a food supply?

The avifauna of Coiba suggests long physical isolation from the mainland. Wetmore (1957) found a high degree of endimism among the birds of the island and the lack of a considerable number of avian families which are known to occur on the mainland.

If there has been a water gap of long standing it is difficult to account for the presence of some of the mammals. Particularly the primates would have found it difficult to cross even a very modest gap. If a land connection once occurred this would seem to solve the problem except that three of the taxa are entirely or largely arboreal and would have required a forested corridor. This does not seem to agree with the avifauna which displays a singular lack of forest families, e.g. Trogonidae, Motmotidae, Bucconidae, Ramphastidae, Dendrocolaptidae. Wetmore has suggested that if Coiba had in the past been joined to the mainland it may have been at a time when there were no forests (and assemblages of forest birds) on the adjacent mainland and that after the island was severed forested conditions came about but the water gap was too great to permit the dispersal of certain avalan taxa present on the mainland. If this is true for birds it must also have been true for arboreal mammals.

The Archipielago de Las Perlas in the Golfo de Panama also possess some interesting features for this discussion. On Isla San Jose a brocket

deer was described by Kellogg (1946) as a new species, viz., Mazama permira which later was given subspecific status, viz., M. gouazoubira permira (Hershkovitz, 1951). No other cervid is known from this island group and this deer is confined to the one island, being absent from the much larger-and closer to the mainland-island of San Miguel. This species of Mazama has at present a very disjunct distribution. It is widely distributed in South America from the State of Sao Paulo, Brazil north to northern Colombia (Cabrera, 1960). Then a markedly disjunct pattern commences with the aforementioned subspecies occurring in the Golfo de Panama and one other subspecies occurring in the northern end of the Yucutan Peninsula. The rest of the suitable Mazama habitat in the Central American Province is occupied by M. americana (assuming all species in this genus are autochthonous to South America) and that the latter preempted the former's habitat. Thus, at the time of the arrival in Panama of M. goauzoubira there may have been a continuous land connection to the islands in the Golfo de Panama over which the animal passed. It is hard to understand, though, why other essentially forest mammalian taxa are not present in the island group, e.g., all the mainland primate taxa; three-toed anteater, Tamanua tetradactyla; tree sloths Choloepus and Bradypus; sciurid rodents; arboreal porcupine, Coendu. Perhaps the animal was once present on Isla San Miguel but was extirpated by aboriginals. If this were the case there should have been no greater chance for survival on the smaller adjacent island of San Jose.

That the San Jose Island brocket may not be particularly well adapted to conditions there is suggested by some of Kellogg's comments made in the original description (1946):

> The hinder upper surfaces of the skulls of both adult males (the types) are irregularly pitted, which may indicate rickets resulting from overcrowding or inadequate diet on this small island.

In addition to the brocket, Kellogg also described as new subspecies from Isla San Jose the following mammals: San Jose Island Agouti, Dasyprocta punctate bellula, and the San Jose Island Spiny Rat, Proechimys semispinosus ignotus = all useful food animals for aboriginals.

Linne (1929) raised the possibility that the pre-Columbian village inhabitants of the big island of San Miguel may have kept tame peccaries penned beneath their raised houses. If this was the case, the animals must have been obtained from the mainland as none have ever been described from the island group.

The San Miguel mammalian fauna is incompletely known (or reported upon in the literature) and the following list is obviously partial (the list is from Bangs, 1901 and includes all taxa except two bats and post conquest introductions of Old World rodents. The taxonomy has been brought into line with that used by Hall and Kelson, 1959): San Miguel Marmosa, Marmosa mitis fulviventer; Island Opposum, Didelphis marsupialis particeps; Island Spiny Rat, Procchimys semispinorosus burrus; San Miguel Cane Rat, Zygodontomys seorsus; Gliding Spiny Rat, Diplomys labilis; Island Tapeti, Sylvilagus brasiliensis incitatus; Island Agouti, Dasyprocta punctata callida. Perhaps all of the just listed mammals arrived in the islands without the assistance of man but some may have been transported.

The avian fauna of the archipelago is fairly well known and Rendahl's list (1920) may be followed. He noted that 26 families present on the mainland are absent in the island group. Of particular interest are avian

taxa which are of importance in aboriginal diets and which are present in the area under discussion. The families Tinamidae (tinamous) and Cracidae (guans and curassows) are of particular importance as food animals to Amerinds. Of the former family the tinamou, Crypturus soui ssp., is present on San Miguel and is said to be identical with the mainland form (Thayer and Bangs, 1905). Representing the family Cracidae is a Chachalaca, Ortalis cinereceps ssp., which the last cited authors indicated does not in any way differ from the bird of the mainland. These two avian taxa may have recently crossed the water gap with no assistance from man (although both families are absent from Isla Coiba which is closer to the mainland than is this group of islands in the Golfo de Panama). There seems to be a good chance that these two species were transported to the islands by aboriginal man. Members of the families Tinamidae and Cracidae are even today frequently kept in a state of partial domestication by the Cuna of the Bayano area of Panama (see Bennett, 1962, for a description of this trait.)

The herpetofauna of the Islands of Panama is too poorly known to permit discussion. However, there appears to be a fairly rich assemblage in the Perlas group of geckonids, iguanids, and teids, many of which are good travelers and often occur as human associates.

Introgressive Hybridization. Through cultural acts which lead to the destruction of barriers between normally allopatric taxa, man may as suggested in the previous chapter, play a role in animal evolution (see Mayr, 1963). Possibilities for this must have occurred during the period of pre-Columbian agriculture. By opening the above postulated corridor of disturbed vegetation into South America certain previously

geographically separated taxa may - from time to time - have been brought into sympatric situations with the possibility of hybridization - if reproductive barriers were not too great. Eisenmann (1957) has drawn attention to such possibilities under currently changing conditions in the Bocas del Toro region of Panama. One wonders if the present subspecific richness of isthmian mammalian and avian faunas is in any way related to such occurrences.

Extirpations. The possibility that human activities during this period may have resulted in some extirpations of faunal elements must be considered. There is no evidence that such did occur but if reference is made to the locally dense human populations that may have obtained for long periods in turn coupled with exploitive pressure of such groups for available animal protein it would appear that some taxa may have suffered. Is, for example, the absence of tapirs, Tapirus , and brocket, Mazama, in western Panama south of the central sierra the result of conditions which do not in any way relate to human land use and faunal exploitation? Land-use patterns which encouraged the production of whitetail deer herds would have had the opposite effect on the last two named taxa. However, those two animals, if they were ever present in western Panama (south of the sierra) should have been able to survive in forested tracts in the higher parts of the Azuero Peninsula and their absence there argues against previous occurrence in the adjacent region.

# Chapter 4

## PANAMA - 1501 to 1903

From the purely historical viewpoint, the four century period extending between 1501 when Rodrigo de Bastidas first sighted the Panama isthmus and 1903 when the isthmian region became the Republica de Panama is a period charged with many events which were of signal importance to the affairs of both the Old and the New Worlds. However, many of these historical events will here be deliberately overlooked and attention will be focussed upon the question as to how the general historic trends of this four century period relate to the ecology and the zoogeography of the isthmus during the same time interval.

As was stressed in Chapter 3, there is a very close relationship between human population size and land-use practices on the one hand and ecological alteration on the other. Thus, attention must first be directed toward an attempt to determine human population sizes and land use during the period under discussion.

The advent of the Spanish presence on the isthmus led to an almost immediate downward turn in aboriginal numbers. This was due to introduced diseases, war, and general bad usage on the part of the Spaniards who used the Indians for labor in mines and fields. Andagoya, writing of early 16th century conditions in Panama (Andagoya, in Cuervo, 1892) was able to point out that well before the mid part of the century Indian populations had become greatly reduced "so that in a brief time neither chief nor Indian remained in the land." (C.F.B. trans.) Actually, quite a few Indians and chiefs remained on the isthmus and Andagoya's

remarks probably refer mainly to eastern Panama which felt first the brunt of the Spanish entrada.

By the early part of the 17th century Indian populations had greatly decreased in eastern Panama and in the islands on the Golfo de Panama as the following remarks from a Relacion of 1607 indicate (Ossejo, ed., 1938 ((1607)) (C.F.B. trans.):

> In another time Chepo had many Indians (but) it has long been diminishing. There are 41 male Indians now. 35 men are married, 5 are widowers, and one is not married. There are 6 widowed women. There are 43 male infants or boys. There are 30 female infants and girls.
>
> * * * * * * * * *
>
> In this (Isla del Rey) there is an Indian town in which the old men assert that there were more than 500 Indians 40 years ago. There has come such a great diminution that today there are no more than 12 male Indians, all married, some to Negroes.
>
> * * * * * * * * *
>
> In the town (on Isla Taboga) there are 14 married male Indians with some sons and daughters.
>
> * * * * * * * * *

The available documents indicate that Indians remained relatively numerous - though vastly declined in numbers as compared with 1500 A D - in western Panama for a much greater period than was the case with the

ezstern parts of the isthmus. There is a note that as late as 1805 Indians were able to muster sufficient force to destroy the town of Santa Fe - later rebuilt (Seemann, 1853.)

The negative influence of disease upon aboriginal numbers was not confined to the sixteenth century for there is evidence that disease was still exacting an important toll late in the eighteenth century. An account of a reconnaissance of northwestern Panama in 1787 (Atencio, 1787, in Cuervo, 1892) contains a reference to a major outbreak of disease ("una grande peste") among the aboriginals in the area which took a large toll of life and sent many of the healthy fleeing from the afflicted region.

The rapid depopulating of Panama caused by the aboriginal demise was not immediately matched by an increase in the numbers of Europeans and Africans - the latter began to be imported into Panama early in the sixteenth century when aboriginal labor became scarce. Thus there was an abandonment, early in the century of conquest, of vast areas which at the beginning of the century has been populated by peoples who practiced shifting cultivation and who hunted and fished.

Unfortunately, census taking during most of this four century period was soo poor as to be all but useless. Therefore attention is directed to the Colombian census of 1832 in which it was indicated that the territory which approximates the present-day Republica de Panama had a human population of 91,785. Eastern Panama (approximately Darien Province and the Comarca de San Blas) counted only 1,425 persons. Allowing for considerable (and probable) error in the census, the eastern Panama total would still be very much less than the 150,000 persons probably present there at the beginning of the sixteenth century.

The 1832 census also indicated that the area to the west of Panama City and south of the western sierra had approximately 75 per cent of the total isthmian population.

The census of 1851 produced a total of 128,897 persons; the 1864 count showed 221,499 persons; in 1880 the count was 307,598 persons (all nineteenth century population data are from Susto, 1960).

The question of land-use must next be considered. In the rural areas of the isthmus crop production was, as it still is, an important activity but most of the activity was at the subsitence level and the techniques employed changed very little in the years after the conquest. Steel cutting tools had replaced those of stone, dibbles were shoed with iron, and fire was more easily kindled but shifting cultivation remained the standard crop growing system. New plants had been introduced by the Spanish some of which such as rice, bananas and plantains were to relegate the older basic food crops of maize and tubers to secondary positions but the new plants were incorporated into the older system of agriculture without any appreciable change in basic land-use patterns.

Of great ecological significance was the introduction of livestock into the isthmian area early in the sixteenth century. Although a number of domesticated animal species were apparently experimented with it quickly became evident that cattle and horses could best survive the physical conditions on the isthmus. Swine were also raised as at present but they were of limited importance. By the early part of the seventeenth century beef cattle husbandry was well established in various parts of western Panama, south of the sierra and cattle herds grazed in the vicinity of the (old) site of Panama City (Oseje, ed., 1938 ((1607)) ). However, the livestock industry cannot be said to have flourished during any part of this four century period with the possible exception of the

very end of the nineteenth century. Thus it appears that only relavively small areas were importantly effected ecologically by livestock during the period here under discussion.

Throughout this period the economy of the mid-isthmian region was - as it still is - dominated not by agriculture or livestock production but by the presence of a convenient pass route between oceans. The treasure from the mines of Peru flowed across the isthmus between oceans. The treasure from the mines of Peru flowed across the isthmus between Panama City and Portbelo until 1746 when it became legal to employ other routes to Spain and the economy of the isthmus fell into a state of decay from which it was particlly rescued in 1850 (Rubio, 1950.)

The discovery of abundant and shallow placer gold deposits in California set in motion a flow of gold seekers many of whom found the ocean route via Panama more attractive than the alternate long journey overland. Sufficient trade was generated to attract financial interests in the United States which led to the formation of a company which constructed a trans-isthmian railroad, 1850-1855 (for an account of these times see Kemble, 1943).

The railroad and the trade it generated brought economic life again to the isthmus but after a few halcyon years another economic decline occurred as the business of the railroad decreased. However, this condition was soon put to flight when a french company obtained a concession from Colombia to construct a ship canal across the isthmus. This precipitated another economic boom which in turn slowed when the French were unable to complete the task. In a series of complicated operations the United States obtained all rights to the canal construction and completed the work in the early part of the twentieth century.

As important - or temporarily unimportant - the pass route was during those centuries it should be remembered that the regions away from the central isthmus were little influenced by the rise and fall of the pass route's fortunes. A subsistence farm economy based on shifting cultivation dominated the occupied portion of thelandscape and livestock and modest crop surpluses provided the limited cash that was obtained. Large tracts of land were not employed for any purpose since there was little population pressure except very locally in parts of west and central Panama.

The reliable ecological inferences to be drawn from the scanty data of population and land use are few but it does appear that there was a large and very significant abandonment of land which at the beginning of the sixteenth century had been occupied by shifting cultivators. The maximum abandonment occurred in the northwest region between the present canal area and Bocas del Toro and in eastern Panama which was all but emptied of human inhabitants in the space of a few decades in the early part of the century of conquest. Large parts of western Panama also were abandoned, especially the footslopes of the western sierra and large parts of the Cocle Plains region.

In the areas of abandonment forests and/or woodlands became reestablished. Darien, which had been opened by the aboriginal farmers went back to forest cover as did the northwest region. Fairly dense woodland appeared in western Panama where once only isolated trees occurred. The route over which Espinosa rode in the early sixteenth century grew up to forest and woodland very different from the landscape he earlier described.

There are few records which permit one to determine the rate of forest regrowth. In Darien, forest appears to have become well established by 1681 in areas which were apparently open at the time of

Balboa's crossing over one and a half centuries earlier (Wafer, 1934). A map of the central pass route region dated 1829 shows patches of land labeled as savanna indirectly indicating that forest was the prevailing feature - this in an area described by Espinosa as being open country several centuries earlier (Webster, 1834, v. 2).

Thus the reduced human pressure on the land led to a radical change in the phytophysiognomy and, by extrapolation, in the pre-existing faunal patterns. The reestablishment of tree cover and the reduction of hunting pressure over large areas must have had the effect of stimulating areal extensions and numerical increases in many forest-associated animal taxa.

On the other hand, the reestablishment of an ocean to ocean forest must have resulted in once again isolating the low second growth and grass land animal taxa of Central America from those of South America. It is of course possible that as the forests of Darien became denser, some taxa aasociated with secondary forest may have moved from South America into the isthmian region as for example the marmoset, Saquinus, which this writer suspects of being closely associated with disturbed forests in the Am climate of central and eastern Panama.

Within Panama, the corridor of disturbed vegetation created by the railroad route may have permitted the dispersal of the whitetail deer, Odocoileus virginiana, from the Pacific side to the Atlantic side (Goldman, 1920). Other animal taxa were undoubtedly influenced by this corridor of grass and low second growth and may have dispersed through it.

In sum, though the period 1501-1903 was for its greater part marked by the ecological retreat of man and the reestablishment of forested or wooded conditions over much of the isthmus. The trend was retarded

during the latter part of the period and then reversed beginning with the modern historical period when a resurgence of human population and new cultural and economic activities led to the mounting of a new ecological assault.

## Chapter 5

## THE CONTEMPORARY PERIOD - 1903 to 1963

For the sake of clarity and convenience the contemporary period of human occupance in Panama is taken to include the time between 1903 and 1963. The year 1903 marks the emergence of Panama as an independent American Republic and the beginning of the U. S. period of canal completion and the later operation of same. Marked ecological changes have occurred during this sixty year period, and continue to occur, more or less as a direct result of a rapid increase in the human population which in turn has led to the intensification of certain land-use practices which are producing profound changes in the present and future land bridge function of the isthmus.

In this final chapter much reliance is placed upon data obtained from a field investigation conducted in Panama by the writer in 1963. Largely of a reconnaissance nature, the investigation was designed to obtain data which would show the nature and degree of the current and recently past ecological attack by man and thus to provide the bases for generalizing on what the altered zoogeographic role of the land bridge is or will soon be.

The first part of the chapter treats with Panama as a single regional entity in order to avoid as much as possible the necessity for lengthy replication of some topical discussions. The past part of the chapter contains a description of what the human influences have been or are during this recent period. To aid in this last the country is divided into four regional units, viz, western Panama, "el interior"; northwest Panama, Canal Zone and adjacent areas; eastern Panama.

Part I

Human Population, 1911 to 1960

The first Panama census of human population, taken in 1911, demonstrated a total of 336,742 inhabitants. The 1960 census taken one half century later recorded a total human population of 1,067,766. The results of the 1960 census are plotted by Distritos on Map 8 to indicate the arithmetic densities prevailing at that time. Attention is directed to the considerable distortion apparent for the Distrito de Panama. Although it appears, on the map, that the entire Distrito is densely settled this is not the case. The human population of the Distrito is concentrated in and around the city of Panama. In western Panama some minor adjustments have been made in the Province of Veraguas to prevent misleading cartographic distortions.

Perhaps the most arresting fact to be derived from an examination of the several Panama censuses is the very great increase in human numbers that has occurred during a brief interval of time. Since the 1911 census the average increase for the Republic has been 15,000 persons per year. Actually this has been accelerating for the annual rate of increase between 1950 and 1960 was approximately 26,000 persons per year. Reference should be made to Table 4 in which are shown some of the recent demographic data for the Republic.

Of particular interest to this study is the growth of human population in the main agricultural areas of western Panama, that is, in the Provinces of Cocle, Herrera, Los Santos, Veraguas (the Pacific side), and Chiriqui. All of these so-called interior provinces doubled or tripled their human populations during the period 1911-1960. The heaviest arithmetic concentrations occur in the areas of Aw climate although areas of Am climate also have subjected to large population increments. It

should be kept in mind that much, and probably most, of this increase has been among the rural poor class which depends chiefly upon crude agricultural techniques to provide a livelihood.

In sharp contrast with the demography of parts of western Panama is the present human population density of Darien Province. The recent total of 19,594 persons scarcely leads to a comment that the area is heavily populated. The province is all but devoid of human inhabitants over large areas which, at the time of the first Spanish entry, were rather heavily populated. The present-day human population tends to be concentrated in the few modest urban areas of the region and, to a lesser degree, along the lower reaches of the major rivers and their tributaries.

Other comparatively empty areas include the higher portions of the isthmus and the Atlantic coastal zone between the Provinces of Colon and Bocas del Toro. The last named province has experienced wide fluctuations in its human population during the last half century (see Table 4.). Most of the fluctuation has been closely associated with the changing fortunes of the banana plantations in the area.

The increasing trend to urban settlement must be noted. This is a phenomenon presently common to almost all of Latin America. In Panama the most spectacular growth has been registered in the capital city of Panama which increased from 74,409 inhabitants in 1930, to 273,440 inhabitants in 1960.

Of great interest is the subject of Amerind demography in Panama. Three groups of aborigines can be recognized in Panama today, viz., Choco, Cuna, and Guaymi. The first two groups occur in areas to the east of the canal and the last group is distributed in parts of western Panama. The recent numbers and distributions of these three groups are

shown in Table 5. (The figures in this last table have also been incorporated in the general table of Panama population but are not separated.) The rate of Amerind population increase has been accelerating in recent years. For the entire thirty year period 1930-1960 the average annual rate of increase was approximately 1.4 per cent. In the last ten year census period, 1950-1960 the rate has been approximately 2.7 per cent. The most outstanding rate of increase has been registered by the Guaymi who average about 2.7 per cent increase per year for the thirty year period and averaged approximately 4.1 per cent annually during the period 1950 to 1960 thus ranking with some of the most rapidly increasing human populations anywhere in the world and exceeding by a significant amount the rate for the Panamanian population as a whole during the same ten years, that is, approximately 2.9 per cent per annum. Standing in contrast is the Choco population which was less in 1960 than in 1930 (assuming a reasonable degree of accuracy for the 1930 census.) This fact is due in part, at least, to the high mobility of the Choco who tend to move rather freely between Panama and Colombia. The Cuna numbers seem to be fairly stable with some increase during the period of record. I am unable to account for the decline between 1940 and 1950. Between 1950 and 1960 there has been an annual rate of increase of only about 1.1 per cent.

The several aboriginal groups tend to congretate into differing sized settlements. Although it is not possible to assert with confidence that settlement sizes are now the same as those at the time of conquest such data are of significance for understanding the ecological relationships of the present. The census data of 1960 which described the size of individual Amerind settlements have been reduced to the data to be found in Table 6. As can be noted, the numerous Guaymi are at present

chiefly grouped into settlements of less than 30 inhabitants and no settlement exceeds 400. In contrast, the San Blas Cuna have several villages which exceed 1,000 inhabitants. The Choco tend to group themselves in small units and at present have the smallest populated units, by size class, as compared with the other aboriginal units now living in Pamana.

The population of the Canal Zone fluctuates according to a number of factors having to do with the state of world shipping and/or world military conditions. The 1960 census listed 41,684 inhabitants of this leased area which was a decrease from the 52,822 numbered in 1950 (U.S. Bureau of the Census.) Canal Zone population is not included in Map 8.

## Land-Use in the Republic of Panama

Crop Agriculture. Of a total employed labor force of 299,386 in 1960 approximately 52 per cent was engaged in agricultural activities (this does not include the aboriginal population. Source: Censos Nacionales de 1960, Republica de Panama.) Of this large percentage most were engaged in crop agriculture mostly at a simple subsistence level.

The main technique followed in crop agriculture in Panama is shifting cultivation or, as it is called in Panama, roza. The basic techniques for this system have been described in chapter 3 thus it is only necessary here to remind the reader that brush and tree removal is a basic feature in which cutting tools - usually a steel machete - and fire are employed in order to prepare plots of land for the sowing of crops. The current techniques employed and their regional variations have been detailed by Guzman in a recent monograph (1956) to which the interested reader is referred.

The annual burning of an increasingly large area of the isthmus is a fact of profound ecological importance. During the latter part of the

so-called dry season, that is, in late March and early April, the smoke rising from the many newly prepared plots is so great that visibility is greatly interferred with. The writer found that during this period of the year it is very difficult to conduct reconnaissance from the air and photography from low flying aircraft was rendered all but impossible by the thick smoke haze.

As the human population in the rural areas of the isthmus grows so to does the area of ecological disturbance. The Panama census of 1960 makes available data relating to the amount of land given over to various food-producing uses some aspects of which are shown in Table 7. As can be noted, in most instances cultivated areas represent rather modest percentages of the total land area in a given province. However, it should be kept in mind that under a pattern of shifting cultivation the area of actual use over a period of years greatly exceeds the quantity represented in a census. In addition there is the very serious problem of locating all the cultivated plots and once having done that there is the problem of determining the size of the plots. Since a large share of the land in crops at any given time in Panama is land that has not been measured and registered to the person using same any agricultural census will of necessity be in error. On the other hand, the figures given in Table 7 probably do represent in a general fashion the relative degree of importance of agriculture from one province to another,

The most important crops are rice (Oryza sativa)and maize, (Zea mays), followed by a host of other plants.

Livestock. The raising of cattle is probably the most important cash producing activity in most of western Panama. The number of cattle has increased dramatically in the years since Panama became independent and this increase has produced and will continue to produce important

ecological changes over large areas. The most favored areas for cattle raising are the Aw climate regions of the Republic. In the early years, according to informants, cattle raising was not particularly profitable because of the distance of markets as well as the poor dry season quality of much of the grazing lands. Therefore, cattle numbers increased slowly never really catching up with the needs of a growing human, and particularly urban, population until very recently. As recently as 1956 (Guzman) it was possible for one writer to indicate that Panama was not self-sufficient in cattle. However, some export has taken place since that time and cattlemen have recently been developing schemes that would increase total consumption of beef.

Of fundamental ecological importance is the phenomenon of introduced pasture grasses in Panama. The most important of these are Faragua (Hyparrhenea rufa), Para, (Panicum spp.) and Guinea (Panisum maximum). The last two named grasses were introduced into Panama in the middle of the 19th century and Faragua was introduced in 1914 (Fuson, 1958). Of the three, Faragua may well be the most important. This is a robust species and prospers in areas where the native grasses sear to the ground during the seasons of reduced rainfall. Cattlemen informed this writer that until faragua became generally available cattle raising was a poor economic venture in many parts of western Panama where today the industry flourishes. This grass is extremely aggressive and once seeded into a pasture tends to become dominant. Thus there is and has been a rapidly increasing area given over to permanent grass cover. Faragua is now a well established plant in all of the Aw climate areas of the isthmus. The other two grasses named above require more moisture than faragua and are better suited to lands in valley bottoms and in moister climatic areas especially those areas of Am climate where cattle are raised.

As indicated earlier, the cattle population of Panama has been undergoing a rapid increase in recent years and this increase has been most pronounced in a few western provinces, viz., Los Santos, Veraguas, and Chiriqui. While it is true that the per cent increase is greater elsewhere than in the just named provinces they together account for nearly 70 per cent of all the cattle in the Republic. In Table 8 some aspects of current and past cattle populations in Panama are shown as well as data on the amount of land presently (1961) being devoted to grazing purposes in the isthmian country. A part of the latter figure must be relegated to livestock other than cattle but since the figure is not broken down in the census it cannot be shown here. However, the bulk of the area in grazing land is given over to cattle as verified by field reconnaissance.

Urban Growth. Major urban growth has thus far been largely restricted to the cities of Panama, Colon, David, La Chorrera, and Puerto Armuelles and these were, at the time of the 1960 census, the only urban areas with human populations of at least 10,000. With the exception of Panama City, the growth of urban centers in Panama tends to be compact with limited tendency for sprawl. The main highway west of the Canal Zone is having some effect upon the form of urban growth with a noteable example to be found in the case of La Chorrera. This city of over 13,000 is very largely a strassendorf especially in the new areas of development.

Panama city is building eastward because its growing human population cannot go west or north being blocked by the Canal Zone and hills. Eastward the level plain extends for many miles and into this area the people have been moving at an increasing rate.

Surface Transportation Routes. Of ecological importance are the nature and distribution of permanent surface routes of transportation.

Very much of Panama is devoid or nearly so of surface routes other than the crudest ox cart tracks, horse trails or foot paths. In eastern Panama and in the Atlantic coastal region away from the canal there are few roads of any kind (except in the banana lands of the Province of Bocas Del Toro). The road net is best developed in the area immediately to the east of the canal, in and around the two canal terminal cities, and in western Panama, "el interior." The few major highways near the canal are paved as is also a large portion of the main highway west of Panama city to Costa Rica. Feeder roads are often only gravel surfaced at best - many of the rural roads are not passable to wheeled vehicles during periods of heavy rain.

The Panama government has long planned to construct a highway through the eastern part of the Republic and thus complete the Inter-American Highway. Should this ever occur it will undoubtedly result in some significant ecological changes in the area crossed by the road.

The Panama Canal. Of great economic importance is the Panama Canal which was constructed across the narrowest part of the isthmus. Begun by a French company in the 19th century, the canal was completed in the 20th century by the U. S. government which has operated the installation ever since and has controlled a strip of land in varying width on both sides of the canal - the Canal Zone. The various installations within the Zone are for the purpose of operating the Canal and areas are given over to a series of urban and military functions. Large parts of the Zone are uninhabited by people. Some agriculture is conducted in the area partly on a cash and subsistence basis.

Part 2

## Western Panama

## Chiriqui Province

It is difficult to separate the recent human-caused vegetational changes in the Province of Chiriqui from those which took place in earlier centuries but the recent growth of human and cattle populations in this most southwestern province of Panama strongly points to major changes having occurred in this century.

Until recently in the modern period the chief assault upon vegetation cover was in the areas of Aw climate since these are most easily converted to pasture lands. More recently, an interest in dairy farming has led to forest removal in C climate areas on the slopes of El Baru. Also, beef cattle production has invaded the moister areas of the lowlands (Am climates). The recent completion to the Costa Rica-Panama border of the Inter-American Highway has made large tracts of hitherto isolated land available for farming and cattle raising or at least has increased the attractiveness of these activities where they previously existed adjacent to the highway route, Some of the area south of the just mentioned highway has been penetrated by roads the most important of which is a road into the Alanje region which is presently the focus of considerable new farm settlement activity which is producing a rapid clearing of forest cover.

It is probably not possible to point to any large part of the Province of Chiriqui and describe the now existing vegetation cover as being of great antiquity (the term "climax" is deliberately avoided.) Small areas of what may be in relatively mature vegetation cover occur at the middle-high elevations and in a rapidly shrinking area in the southwestern part

of the province. In the latter areas isolated forest trees with trailing lianas and heavy loads of epiphytes are increasingly common as the area is cleared for farms and cattle pastures.

David Area. The area of maximum vegetation disturbance is centered on the capital city of the province, David. In this zone the vegetation exhibits many fire and drought resistant forms and grass cover is very extensive. A common feature is the many "chumicales" - areas covered with dense thickets of chumico, Curatella americana. These thickets are found where burning is an annual occurrence and there the dry season of the Aw climate is especially well developed. Of course, chumico is generally distributed in the seasonally drier parts of the province. Also, seemingly closely related to fire when found in fairly heavy stands is maranon, Anacardium occidentale. This last is a common tree-shrub in the Aw areas. A third very common tree-component of the drier areas of fire disturbance is malagueto, Xylopia spp. whose curiously drooping leaves are very distinctive. Scattered through the trees just mentioned is the drought and fire resistant nance, Byrsonima crassifolia. No part of this zone has not been repeatedly disturbed by man for a very long time.

To illustrate in part the nature and areal arrangement of vegetation disturbance in the central part of Chiriqui a highway transect from the near sea level to almost 4,000 feet elevation produced the following results:

Begin at Pedregal (approximately 4 miles south of David)

Elevation 10 feet. On land above tidal influence (this lower area is covered by mangrove) there is a high percentage in grass cover, chumico, and isolated small stands of trees of several genera. This region very likely was in forest not very many years ago as is indicated by tree remnants but the impact of repeated burning and the introduction of

faragua grass has converted the land to permanent pastures.

David (north edge)

Elevation 205 feet. This is in artificial pasture in which imported grasses compete with tree and shrub species just mentioned above. In this area live fences are common and contain several genera such as Bala, Glircidia septium, carate, Bursera simaruba, cacique, Diphysa robinoides, maranon, Anadardium occidentale.

Elevation 350 feet. Heavy stands of chumico, and some grass.

Elevation 680 feet. Malagueto common to abundant as is maranon. Roadside trees include malagueto, carate, maranon, higueron, Ficus spp., guanabana, Annona spp., cacique. There are some palms in the pastures and fields and, where there is abundant surface moisture, espave, Anacardium excelsum.

Elevation 1,300 feet. Artificial pasture, a few palms and maranon is almost the only roadside tree species present.

Elevation 2,000 feet. Heavy stands of chumico with some nance and maranon. Much evidence of recent burns.

Elevation 3,200 feet. Sparse tree cover which is mostly nance. Ciqua, Nectandra spp., and grass are present.

Elevation 3,700 feet. (Top of grade on road to Boquete.) A grassland with scattered low trees which are mostly nance. The height of the tree cover is seldom more than 15 feet with an average of approximately 10 feet. The trees are markedly deformed by the dry-season down-slope winds. The trees bend down slope and their maximum growth is also in that direction. The grass is chiefly faragua. The soil is very thin and stony with much volcanic material.

n.b. At approximately 1,900 feet elevation there is a small grove of trees some of which exceed 60 feet in height A few small surface streams cross the area of the grove through the entire dry season and this probably accounts, in part, for the presence of the grove although it is presently given protaction from fire and clearing. The tree genera recognized included espave, Anacardium excelsum, higueron, Ficus spp. malagueto, Xylopia spp., nance, Byrsonima crassifolia,guarumo, Cecropia spp., limon, Citrus spp., mango, Mangifera spp. The last two genera are exotics and their presence together with Cecropia clearly indicate the disturbed nature of this grove.

Avian taxa were also observed and noted for several parts of the transect just described with the following results (dry season, 1963):

Pedregal area.

Grass: Variable Seed-eater, Sporophila aurita; Ruddy-breasted Seed-eater, Sporophila minuta; Green-backed Sparrow, Arremonops conirostris; Meadowlark, Sturnella magna; Red-breasted Blackbird, Leistes militaris.

Elevation 3,200 feet. Grass, nance, cigua. Thin, rocky soil. Trees are short and do not provide continuous cover.

| | |
|---|---|
| Wood Quail | Odontophorus sp. |
| Lesser Nighthawk | Chordeiles acutipennis |
| Rufous Nightjar | Caprimulgus rufus |
| Plain Wren | Thryothorus modestus |
| Clay-colored Robin | Turdus grayi |
| Ani | Crotophaga sp. |
| Yellow-crowned Euphonia | Tanagra luteicapilla |

| | |
|---|---|
| Blue-grey Tanager | Thraupis episcopus |
| Yellow-bellied Elaenia | Elaenia flavorgaster |
| Meadowlark | Sturnella magna |
| Green-backed Sparrow | Arremonops conirostris |
| Variable Seed-eater | Sporophila aurita |

Elevation 3,800 feet. Grass and sparse low tree cover.

| | |
|---|---|
| Black Vulture | Coragyps atratus |
| White-collared Swift | Streptoprocne zonaris |
| Grey-breasted Martin | Progne chalybea |
| Meadowlark | Sturnella magna |
| Blue-grey Tanager | Thraupis episcopus |
| Green-backed Sparrow | Arremonops conirostris |
| Rufous-collared Sparrow | Zonotrichia capensis |

No trapping for mammals was done and few were observed in the area of the transect. In the hours just before sunrise a lagomorph, which was probably Sylvilagus brasiliensis, was often encountered at almost all elevations. An oppossum, Didelphis marsupialis which had been killed by a motor vehicle was observed at approximately 3,500 feet elevation. Hunters indicated that the only game mammal in the area of the transect is the white tail deer, Odocoileus virginiana, and this is exceedingly scarce at present.

Boquete area. Land-use in the highland area of Boquete is varied but agriculture of several kinds dominates the scene. Coffee production supplies the single most important cash crop but truck farming is also of great economic importance. Because the raised elevation produces a moderation of tropical temperatures the Boquete region is one of the most important resort and recreational areas in Panama.

The most important recent removal of forest vegetation in this area is related to the growth of coffee plantings and to discover some of the

environmental changes associated with such alterations two recording hygrothermographs were installed so that one measured ground (first 12 inches) conditions within a forest remnant and the other measured conditions at the same level in a cleared area. Although the record is very short it is sufficient to show that fairly large temperature differences are to be expected at the two kinds of locations. The time of observation coincided with the dry-to-wet season transition period and, therefore, the humidity record is not representative of the dry season. The data from these observations appear in Table 9.

Virtually no forest remains below the 4,000 feet level. Above 5,500 feet forest disturbance in the Boquete area is presently very slight although just to the west, near Cerro Punta at approximately 7,000 feet, large tracts of montane forest have recently been removed to make pasture lands for dairy herds. In the coffee growing areas it is customary to leave some trees for shade although in recent years there has been a trend toward planting coffee tree varieties which do not require shade.

Avian taxa commonly observed inside areas planted to coffee were observed and recorded as follows:

Coffee Finca at approximately 4,000 feet.

| | |
|---|---|
| Squirrel Cuckoo | Piaya cayana |
| Clay-colored Robin | Turdus grayi |
| Blue-grey Tanager | Thraupis episcopus |
| Scarlet-rumped Tanager | Ramphocelus passerinii |
| Baltimore Oriole | Icterus galbula |
| Rufous-collared Sparrow | Zonotrichia capensis |
| Green-backed Sparrow | Arremonops conirostris |
| Flycatchers | Fam. Tyrannidae |
| Woodpeckers | Fam. Picidae |
| Hummingbirds | Fam. Trochilidae |

Trapping for mammals was not done and the list of mammals for the Boquete region was obtained through interrogation of hunters living in the area:

| | | |
|---|---|---|
| *Shrew | Cryptotis sp. | |
| White-face Monkey | Cebus capucinus | |
| Red Spider Monkey | Ateles geoffroyi | |
| Black Howler Monkey | Alouatta villosa | |
| *Nine-banded Armadillo | Dasypus novemcinctus | |
| *Forest Rabbit | Sylvilagus brasiliensis | |
| *Tree Squirrel | Sciurus variegatoides | |
| Paca | Agouti paca | |
| *Agouti | Dasyprocta punctata | |
| Otter | Lutra annectens | |
| Puma | Felis concolor | |
| *Coati | Nasua narica | |
| *Tayra | Eira barbara | |
| Tapir | Tapirus bairdii | very rare |
| Collared Peccari | Tayassu tajacu | rare |
| White-lipped Peccari | Tayassu pecari | rare |
| Brocket Deer | Mazama americana | rare |

Taxa preceeded by * also occur commonly within areas disturbed for coffee planting. The other taxa appear to be confined to the forested tracts up to at least 7,000 feet elevation.

All informants insisted that whitetail deer do not occur in the highland region though it is well known at lower elevations (though now rare.) All informants also insisted that no primate matching the description of the marmoset Saguinus is known in this region.

David west to Panama-Costa Rica Frontier. The highway west from David to the Costa Rica border cuts through an area which is being increasingly disturbed because of the presence of the highway. The vegetation along this route is described below.

At the western edge of David the country is in open artificial pastures and the few trees present are very often exotic species which are grouped in little clusters adjacent to residences. With increasing distance westward increasing amounts of land is given over to roza farming and the low second-growth of trees and shrubs associated with such land use becomes increasingly abundant. In the neighborhood of the town of Concepcion a climatic boundary is passed with visible indications that there is more moisture here in the dry period than in the area to the east. Second-growth patches of trees and shrubs now increase and palms become frequent. The last are deliberately spared to provide thatching material as well as raw material for the manufacture of a crude wine. For this latter use the tree - probably Acrocomia vinifera - must be felled. As evidence of the increasing amount of soil moisture encountered with increasing distance westward are the large numbers of platanillo, Heliconia spp. (Musacae) which line the roadside and appear as an early seral stage in abandoned rozas. In Panama generally, the writer did not observe Heliconia in areas of Aw climate and it may be taken as a good indicator of humid conditions at least as moist as those obtaining usually in Am climatic regions. Also appearing with great frequency in disturbed plots is balsa, Ochroma lagopus, this taking over from guarumo, Cecropia spp. which is a common second-growth tree in almost all climatic situations but seems to not to compete as well as Ochroma where the two occur where the vegetation has been disturbed by man in moist regions.

Westward from Concepcion there is an increasing number of small tracts of less than an acre (less than one-half hectare) of forest that have not yet been felled. Although most of the tree taxa were not identified, espave, Anacardium excelsum appears to be very common and ceiba, Ceiba pentandra were also occasionally noted with trailing lianas and desicating burdens of epiphytes - chiefly bromeliaceae. The land use is given over to cattle raising as well as roza farming.

The wide - and increasing - corridor of forest removal continues without interruption to the border and beyond into Costa Rica and thence westward at least 58 miles to Palmar. The road in Costa Rica has only recently been completed and is now an avenue for new farm settlement which is producing the same conditions just described for Panama. In time, a corridor of grass and second growth vegetation will connect Chiriqui Province with Guanacaste Province of Costa Rica and thus there will be a long corridor of disturbed vegetation extending from southern Mexico to and perhaps beyond Panama,

Between David and the border the finches previously listed for the area between Pedregal and the upper slopes of the road between David and Boquete also occur. Also common are: White-tipped Dove, Leptotila verreauxi; Ruddy Ground-dove, Columbigallina talpacoti. In the moister tracts of second-growth trees Scarlet-rumped Tanagers, Ramphocelus passerini are common. Over open lands flycatchers (fam. Tyrannidae) are common. The grass cover provides shelter for Meadowlarks, Sturnella magna, while beside the road, Ani, Crotophaga sp. are very abundant.

Between David and Alanje the land is chiefly used for cattle pasture. Fields and (dirt) roads are lined by various tree species of which carate, Bursera simaruba, is the most abundant. The pasture grass in this area appears to be mostly faragua although in moister areas para and guinea appear.

Beyond Concepcion the moister country noted above prevails with the same type of disturbed vegetation and land use. Throughout this area finches, particularly Sprophila, are very abundant. Just before the banana plantations are entered there are a few forest remnants to be seen giving testimony to the conditions that existed up until just a few years ago.

Within the banana lands all evidence of the pre-existing vegetation cover has been erased and the land is given over entirely to the production of bananas or to the production of crops and beef for the local labor. The plantations contain a number of settlements which serve to house plantation workers and their families. Birds noted within the bananales include: Scarlet-rumped Tanagers which were very common; Blue-grey Tanagers, also very common; Ani, common; Variable Seed-eaters, common in all grassy locations; Giant Cowbird, Psomocolax (=Scaphidura) oryzivorus, common in open areas; Ruddy Ground Doves, everywhere abundant; Cattle Egrets, Bulbulcus ibis, seen almost everywhere that cattle appeared in pastures.

Banana land workers were agreed that Squirrel Monkeys, Saimiri oerstedi, are abundant in the banana plantings and are never encountered in the small tracts of forest mentioned above. All attempts on the part of the writer to view these little primates in this area failed. Time did not permit the compilation of a reliable list of game mammals present.

David east to provincial boundary at the Rio Tabasara. From David east to the town of Chiriqui the land is in pasture and chumicales and no clear indication to the original vegetation is visible. Just to the east of the town of Chiriqui the countryside begins to take on the signs of

slightly greater moisture - signs that increase with increasing distance eastward. Patches of woodland appear in man-made pastures and low second-growth vegetation associated with roza farming become increasingly apparent. Infrequent large isolated trees give evidence as to what kind of vegetation cover recently occurred in the wetter areas which are now given over to cattle pasture. In the vicinity of Remedios, now by-passed by the new highway, enough of the forest survives in the cattle pastures and roza lands to clearly indicate that the area would soon go back to forest cover if man were to abandon the land. Similar conditions continue adjacent to the highway until the provincial border is reached.

North of the highway route and not visible from the road is a great swath of land aligned more or less parallel with the Sierra throughout which the vegetation has been greatly disturbed and almost no forest vestiges remain - even in the moister areas. This must be the result of aboriginal land use since pre-contact time. It is in this area that most of the Guaymi Indians of the Province of Chiriqui presently live and their present number is most certainly a fairly modest fraction of the number that was present in the early part of the sixteenth century. The appearance from the air is one of great ecological destruction of which vegetation removal, repeated burnings and accelerated soil erosion are the most conspicuous elements. Tole, one of the largest settlements of this zone, is located in the midst of great apparent man induced ecological poverty.

Human Influences on the Zoogeography of Chiriqui Province. The chief recent human influences on the zoogeography of Chiriqui Province are related to the major vegetation alteration that has taken place in the last few decades. This has had the immediate effect of greatly reducing or locally extirpating all animal taxa which are strictly forest or woodland inhabitants. If the present trends in tree removal continues for another two decades forests will no longer exist at all in the lowlands of the province

and will be restricted to the highest elevations in the highlands.

Animals which appear to have benefited by the new conditions include chiefly avian taxa of which the finches (Fringillidae) are most prominent. As was noted repeatedly above in local descriptions, seed-eaters invade man-created grasslands in a wide variety of elevations and climatic conditions. In fact, it appears that insofar as the lowlands are concerned, climate is of no appreciable importance in the distribution of many of the fringillids but rather the presence or absence of seed-bearing grasses seem to be the chief controlling factors to dispersal. Some of the open country seed eaters appear able to disperse through the narrowest of man-created corridors and will, for example, disperse along the strips of grass growing beside roads which have been constructed through forested areas.

Destruction of forests and woodlands has greatly restricted the ranges of the several primates, Alouatta, Cebus, Saimiri, which formerly were widespread in the lowland woodlands or forests of the province. These genera are now confined, in the lowland areas, to small tracts adjacent to the littoral and especially on the islands just to the south of David.

Hunting pressure on game bird and mammal populations in the province has become extreme and, particularly in the lowlands, hunting is often considered a wasted effort. Whitetail deer have become rare except in the area near Remedios and even there it is by no means abundant. In the highland area tapirs have become very rare wherever there is any appreciable hunting effort although spider monkeys remain fairly abundant even though much sought after for food during some parts of the year.

In sum, it may be asserted that Chiriqui Province has rapidly become a 'savanna' land in the elevations below 4,000 feet and that the exceptional areas remaining in forest will, in the next few decades, also be in a similar condition. The destruction of former physical barriers between

allopatric populations leads to the possibility of hybridization among taxa not separated by reproductive distance. The opportunities for extensive latitudinal dispersals are numerous although hunting pressure by man restricts some of these possibilities at present.

## Veraguas Province

Large areas of Veraguas Province are now very sparsely inhabited by man - especially the Atlantic coast region which will be included in the discussion of the northwest region of Panama. The Island of Coiba is a penal colony and thus is all but empty of humans. The western slope region of the Azuero Peninsula is also lightly inhabited although this is an area into which people are presently moving.

Elsewhere in the province the human population distribution is fairly evenly distributed excepting, of course, the several larger settlements of which Santiago (1960 pop., 8,746) is the largest.

The economic base of the province consists of cattle raising and agriculture with the latter being chiefly of the roza type. The cattle industry provides the single largest source of cash income for the area.

Veraguas Province was well populated at the time of Spanish contact and much of the presently visible ecological alterations must have occurred or were begun in the pre-Columbian period. However, a more recent ecological attack has been taking place resulting in a removal of forest cover that had become established after the great reduction in aboriginal populations which took place shortly after the conquest. It is to this recent period that attention is largely directed below.

Santiago to Santa Fe. An air transect between Santiago north to Santa Fe (which was not accessible by road at the time of the investigation)

produced visual evidence that this area has been maximally disturbed by man, and, in view of the present modest and dispersed human population in the area, it must be concluded that an appreciable amount of the vegetation destruction occurred in aboriginal times. Instead of the forests that might be expected here there are grass and a few scattered trees. Thin bands of culturally-induced gallery forest appear beside some of the permanent streams the most notable of which are tributaries of the Rio Santa Maria.

Santiago west to Rio Tabasara. An air transect west of Santiago to the provincial boundary at the Rio Tabasara indicated that the conditions already described for the eastern end of Chiriqui Province continue without interruption into Veraguas. The chief feature noted in addition to the just mentioned aspects was that moisture conditions between Santiago and the Rio Tabasara change rapidly in the dry season from conditions of pronounced desiccation in the vicinity of Santiago to increasing moisture westward.

Santiago - Sona - Bahia Honda (located on the west coast of the Sona Peninsula.) An air transect which has as its chief aim the reconnaissance of the peninsula south of Sona revealed that the peninsular region, though apparently very recently covered by forest, is now undergoing rapid tree removal as new settlers invade the area searching for farm land. This human invasion has already resulted in a severing of the previously continuous coastal forest corridor which once joined the similar forests of Chiriqui Province with the forests of the Azuero Peninsula. Now, the western shore area of the Golfo de Montijo is in cattle pasture with rapidly decreasing isolated stands of forest trees. In these areas palms are conspicuously abundant being preserved for the same reasons as those advanced to account for the practice in Chiriqui - thatching and wine. In the

center of the peninsula of Sona and along its west coast, particularly in the vicinity of Bahia Honda, heavy forest marches almost to the beach line. These conditions will not last for long as the entire peninsula area will soon be invaded by roza farmers and stockmen.

Santiago south to Southwest Tip of the Azuero Peninsula. An air transect made over the western slope region of the Azuero Peninsula revealed that this area, though lightly populated at present, is being invaded by farmers from the north and each of the numerous river valleys has had a large amount of forest removed to make way for farming and livestock. Extremely isolated though this area is, it has not prevented a remarkable amount of tree removal from taking place. This was especially noticeable in the northern part of the Azuero region where the forests on slopes have retreated very appreciably in just the last ten years. In the northwestern corner of the Azuero Peninsula, that is, near the head of the Golfo de Montijo, recent forest removal has resulted in the complete isolation of the Azuero forests from similar vegetation cover elsewhere in mainland Middle America.

Central Veraguas. From Santiago eastward, the climate becomes more pronouncedly Aw and land use is given over increasingly to cattle raising although roza farming never completely disappears and in some locales remains important. Extensive tree clearing and the annual use of fire has created a phytophysiognimic aspect very similar to the areas in the vicinity of David, Chiriqui Province. Roadsides are characteristically lined with tree fences containing now familiar genera such as carate, Bursera simaruba; macano, Diphysa robiniodes; jocote, Spondias spp.; Maranon, Anarcardium occidentale. In the pastures Nance, Byrsonima crassifolia, is very abundant as is also Chumico, Curatella americana, especially where soils are thinnest and burning most pronounced. In

many parts of the central portion of Veraguas there would be almost no trees at all were it not for the roadside fences.

The Ponuga area. The area at the northwest end of the Azuero Peninsula is illustrative of some of the recent ecological changes caused by man in the Veraguas area and here, on a cattle and rice finca, two recording Bendix hygrothermographs were set in operation to measure temperature and humidity conditions within tree cover and over artificial pasture. A very short dry season and an equally short wet season record was obtained for the purpose of determining what differences, if any, occur between the two habitats. The results are shown in Table 10. Unfortunately, the so-called dry season of 1963 was poorly developed in this area and the data, therefore, are limited in value. As would be expected, the diurnal temperature range is somewhat greater in the pasture area than under tree cover.

The area comprising the finca was thirty years ago almost entirely in heavy forest. Even as recently as the 1958 dry season when the writer visited this immediate region where were heavy forests nearby on the hill slopes and the calls of howler monkeys were heard daily. This forest has now disappeared and, of course, so have the monkeys. Thirty years ago, whiteface monkeys, Cebus, and howler monkeys, Alouatta, were common in areas which are today devoid of trees and given over to artificial pasture or rice culture.

During the period of reconnaissance (part of the dry season 1963) the following birds were commonly seen in the cleared lands of the Ponuga area:

| | |
|---|---|
| Fork-tail Flycatcher | Muscivora forticata (migrant) |
| Variable Seedeater | Sporophila aurita |

| | |
|---|---|
| Ruddy-breasted Seedeater | Sporophila minuta |
| Ani | Crotophaga sp. |
| Orange-chinned Parakeet | Brotogeris jugalaris |
| Red-legged Honeycreeper | Cyanerpes cyaneus (in gallery) |
| Tropical Kingbird | Tyrannus melancholicus |
| Yellow-headed Caracara | Milvago chimachima |
| Ruddy Ground Dove | Columbigallina talpacoti |
| Wood Quail | Odontophorus sp. |
| White-tipped Dove | Leptotila verreauxi |

Hunters living in the Ponuga area supplied the data for the following list of game mammals:

| | | Status |
|---|---|---|
| Virginia Oppossum | Didelphis marsupialis | Cac |
| Nine-Banded Armadillo | Dasypus novemcinctus | Cac |
| Forest Rabbit | Sylvilagus brasiliensis | Cfr |
| Agouti | Dasyprocta punctata | Rfr |
| Paca | Agouti paca | Rfr |
| Tree Squirrel | Sciurus variegatoides | Rfr |
| Ocelot | Felis pardalis | Rf |
| Puma | Felis concolor | Rf |
| Jaguar | Felis onca | Rf |
| Coati | Nasua narica | Rfr |
| Otter | Lutra annectens | Rw |
| Whitetail Deer | Odocoileus virginiana | Rr |
| Collared Peccary | Tayassu tajacu | Rfr |
| White-lipped Peccary | T. pecari | Rf |

(C = comm1n; ac = all of vegetation cover; f = forest;

r = rastrojo or second-growth shrub; R = rare.)

All informants insisted that brocket deer (Mazama) and tapirs (Tapirus) do not occur in the area nor is there any record of their having occurred in the area at some time in the past.

Human influences on the Zoogeography. The ecological alteration long ago begun by the aboriginal occupants of the foothills of the central sierra of the Pacific slope of Veraguas is now being rapidly extended by non-aboriginal peoples in their desire to extend the area given over to cattle raising and roza farming.

One effect of this recent activity has been to isolate most if not all of the older forest-associated animal taxa of the Azuero Peninsula from all other forested areas of Panama. Until this century an avenue of coastal forest (not including the still-present mangrove) connected the Azuero region with the Chiriqui area and, probably, adjacent forested areas of Costa Rica. This corridor was apparently never very wide but possibly did permit the dispersal through it of the primate genera Ateles, Cebus, and Alouatta, a dispersal that may have been from west to east. That the corridor was narrow is suggested by the lack of Mazama and Tapirus in the Azuero area. The night monkey, Aotus, may have dispersed through more open woodlands from the central sierra (a route that may have been followed by the other three primate genera mentioned above.) Aotus probably did not disperse from western Panama as the taxon is not known from west of the Azuero region.

The incompletely known avifauna of the forested tracts of the Azuero region may also have moved through the previously existing coastal forest corridor.

The opening of lands to grass has, as in Chiriqui, stimulated th dispersal of various animal taxa which find the new conditions acceptable. Chief among such taxa are the finches, Fringillidae.

Extreme hunting pressure maintained for the last three decades has resulted in the virtual elimination of formerly common to abundant game mammal taxa. At present, the larger game mammals have become so scarce in the more (human) populated areas as to render hunting little more than an excuse to take part in recreation away from regular farm tasks. As recently as fifteen years ago it was common for men of the Santiago, Ocu, and Ponuga areas to add to their income through market hunting - chiefly for whitetail deer. By 1960 such activity had virtually ceased due to the extreme paucity of game.

As the drive into the western Azuero region continues the area of forest and its associated fauna will shrink to a small remnant more or less coincident with the higher elevations in the south around Cerro de Cambutal.

Provinces of Cocle, Herrera, and Los Santos

The combined areas of the three west central provinces of Cocle, Herrera and Los Santos (excepting the southwest corner of the last) form a natural unit of climate, landforms and culture history. As indicated in earlier chapters, this is an area of grasslands, woodlands and shrublands virtually all of which owe their present physiognomy to the long-term cultural activities of man. At the time of the first Spanish entry into the area ecological disturbance had reached an advanced stage. Rapid depopulation following upon the period of contact led to a partial re-establishment of tree cover and this has in recent decades undergone a process of clearing which is now in a very advanced state.

Most of this region experiences an Aw climatic regime and the annual period of reduced precipitation (usually mid-December to mid-April) is accompanied by a continuous blast from the northeast trade winds which in their descent from the central sierra are warmed adiabatically and are,

therefore, desiccating in their effect. Only the space of a couple of weeks is required to change the wet season green countryside to dull browns and yellows with swirling dust clouds where there is no plant cover. Toward the end of the dry period farmers and cattlemen set the land ablaze turning the air into a thick haze and the land to the color of ash. Burning is now more controlled than in past years but is still so great as to effect large areas of the poorer pasture and roza lands.

During the early years of the Republic of Panama surface transport connecting the central region with the capital city, Panama, was very poorly developed and this fact coupled with the then poor quality of native pasture grasses acted as a braking affect upon the development of the cattle industry and thus retarded the destruction of the re-established tree cover. When surface transport was improved and pastures improved through introduction of the panic grasses and the hardy faragua there was new inducement to turn to cattle raising. Land given over to roza farming also increased as the human population of these central provinces increased. The ecological changes associated with the recent cultural changes have been on a large scale.

In the Aguadulce area thirty years ago there were tree stands of impressive size where there are no longer any trees. In the Ocu area there has been a similar recent removal of trees to make way for new pastures of faragua grass. Similarly changed conditions are found south along the eastern end of Los Santos Province to beyond Pedasi. Today, viewing this region from the air, or ground, it is difficult to discover other than the faintest suggestions that this was recently in tree cover.

This is not to say that no trees remain. In the flood plains of the rivers crossing the region dense though isolated stands of trees are common and in some local areas where there is a high water table away from rivers the pastures may contain many trees. Also scattered throughout the

cattle lands are little tree patches growing upon little rises of volcanic materials upon which the soil is too poor to justify the effort of clearing for crops or pasture.

Shore of Golfo de Parita Northwest Through Aguadulce to the Sierra. Typical phytophysiognomic conditions of much of the central province area may be illustrated with a transect of vegetation from the shore of the Golfo de Parita northwestward to the central sierra.

The vegetation of much of the area regularly subjected to tidal influences is mangrove of which Rhizophora, Conocarpus, and Laguncularia are particularly conspicuous. This formation is exploited by charcoal makers but only occasionally is a stand found where such exploitation has resulted in obvious impoverishment of the tree populations.

On the landward side of the mangroves and at the tree line of the beach the Manzanillo, Hippomane spp., with its very toxic sap commonly occurs along with a cactus, Pitahaya, Acanthocereus pentagonus, whose fruit is gathered in season. Above the tide line and in less saline soils than occur in the just previously mentioned areas there is usually a dense thicket of low trees and shrubs many of which are armed. Not all the genera were identified but the following partial list will serve to indicate the general floristic nature of this formation: Prosopis; Acacia; Hamellia; Gliridida; Bromelia.

Landward of the thorn-bush thickets, pasture lands appear in which there are scattered various tree and shrub genera of which the following are typical: Anacardium occidentale; Byrsonima; Pithecolobium; Curatella; Cochlospermum; Sterculia; Diphsa; Tabebuia; Enterolobium; Bursera; Xylopia.

As greater proximity to the central sierra is gained trees become increasingly rare and grassland come to dominate large areas of what must be an old culturally disturbed landscape. Although exceedingly variable, the

upland forests usually commence at about the 4,000 feet elevation level.

In places of human settlement, whether it be a single farmstead or an urban area, there is usually a large collection of trees and palms which often include exotic taxa. Roadsides are often lined with a thin row of trees which in this area are often of the following genera: Spondias; Anacardium; Bursera. The fruit of the Spondias spp., though often utilized elsewhere in Central America, are here generally not harvested though perfectly edible.

Penonome - Anton area. Beginning a little to the west of Penonome and extending in a broad swath east to, and well beyond, Anton, is a zone of extremely disturbed vegetation that owes its character to a long history of burning, severe edaphic conditions and pronounced dry season desiccation. Although it is tempting to characterize this zone of poor grass and sparse shrub cover as a climatic savanna it would, if protected from burning and incredible overgrazing, revert to at least a shrub cover in which Anacardium occidentale, Curatella americana, and Byrsonima spp. would be very abundant, for these manage to survive in sometimes large stands in spite of the long-term ecological assault that has occurred in the area. To be sure, there are some small areas just to the east of Penonome where the soil has been so badly eroded not even grass is presently able to become established.

Aguadulce-Chitre-Las Tablas-Pedasi. The arcuate portion of the central provinces extending from Aguadulce to Pedasi is possessed of a phytophysiognomic character very much like that described above for the Aguadulce area. Gallery forests intersect the region - forests which are largely man-created and being no more than thin lines of trees that have been permitted to remain beside the streams. Even these collections of trees are often disturbed, however, and bare river banks are by no means rare as, for example, along stretches of the Rio de La Villa near Chitre. In the dry

shrub formation seaward from Chitre there are local stands of an Opuntia spp. which does not agree with the characters given for O. elatior - the only member of this genus which has thus far been described from Panama. If it is a different species it may have been introduced during the period when cochineal culture was significant in the Middle American area.

Rio Tonosi Valley. Standing in sharp geographic contrast with the just described central province area is the valley and adjacent areas of the Rio Tonosi located in the south of Los Santos Province. This region has an Am climate and largely because of its long geographic isolation south of the southern Azuero uplands has not, in the post-contact period, experienced the ecological attack that has been described for the other parts of Los Santos Province.

The chief areas of significant vegetation disturbance occur in the lower part of the Tonosi river valley in which the town of the same name is centrally located. Agriculture is poorly developed and virtually the only type followed is that of roza cultivation. There are very few livestock animals in the area due to limited pasture and a limited local market. In 1963 there was a small amount of forest exploitation on the more accessable slopes of Cerro Cambutal from which it was said that mahogany, (Swietenia) was being removed during the short dry season.

The long isolation of this region was overcome in the latter part of 1963 when an excellent all-year road was completed to the town of Tonosi. This is certain to produce cultural activities which will result in a major forest removal in this region as the pressure on farm land elsewhere in Panama stimulates settlement in the valley. The soils though heavy, tend to have very high calcium contents derived from limestone parent materials.

In the immediate vicinity of Tonosi there were some isolated stands of forest that had not yet been destroyed to make way for farm or pasture and these tracts gave an opportunity to observe some of the faunal elements

able to survive for long periods in such 'islands' of vegetation in the midst of cultivated landscapes.

The vegetation in this 'island' stand was growing on a heavy clay soil that gave every indication of being waterlogged during the long nine month annual period of heavy precipitation. In March the soils had cracked badly even in the deepest shade of the forest. Only a few trees were identified as to genus but one taxon, Espave, Anacardium excelsum, was by far the most abundant species. Under the story of low branching trees there was a layer of palms of which many were armed. That part of the detritus resting upon the ground which was derived from armed palms made passage through the forest extremely difficult as the spines passed through all but quite heavy leather. Leaf litter was abundant and made a silent passage through the trees virtually impossible.

Mammals observed within the forest were: Cebus; Alouatta; Sciurus; Dasyprocta. Several bands of Alouatta were frequently observed and the Cebus population appeared to be high though no reliable count was obtained. Sciurus was frequently observed within the forest as well as in second-growth and tree lines well removed from the dense tree cover. Dasyprocta appeared to be fairly abundant although they are much hunted in the area.

Birds observed inside or at the forest edge included the following:

| | | |
|---|---|---|
| Squirrel Cuckoo | edge only | Piaya cayana |
| Little Tinamou | | Crypturellus soui |
| Savanna Hawk | edge only | Heterospizias meridionalis |
| Orange-chinned Parakeet | | Brotogeris jugularis |
| White-tipped Dove | | Leptotila verreauxi |
| Red Lored Parrot | | Amazona autumnalis |
| Mealy Parrot | | Amazona farinosa |
| Ani | edge only | Crotophaga sp. |
| Screech Owl | edge only | Otus sp. |

| | |
|---|---|
| Black-throated Trogon | Trogon rufus |
| Slaty-tailed Trogon | Trogon massena |
| Blue-crowned Motmot | Momotus momota |
| Clay-colored Robin | Turdus grayi |
| Semi-collared Nighthawk | Lurocalis semitorquatus |
| Streaked Flycatcher | Mylodynastes maculatus |
| Black-chested Jay | Cyanocorax affinis |
| Hummingbirds | Fam. Trochilidae |

In cleared areas the following birds were noted:

| | |
|---|---|
| Variable Seed-eater | Sporophila aurita |
| Tropical Kingbird | Tyrannus malancholicus |
| Wood Quail | Odontophorus sp. |
| Ani | Crotophaga sp. |
| Crimson-backed Tanager | Ramphocelus dimitiatus |
| Snowy Egret | Leucophoyx thula |
| Black Vulture | Coragyps atratus |
| Turkey Vulture | Cathartes aura |

Interrogation of hunters in the Tonosi area produced data for the following list of larger mammals said to occur in the region:

| | Status | |
|---|---|---|
| White-face Monkey | common | Cebus capucinus |
| Howler Monkey | common | Alouatta villosa |
| Spider Monkey | rare | Ateles geofroyi |
| Otter | rare | Lutra annectens |
| Coati-mundi | rare | Nasua narica |
| Ocelot | common | Felis pardalis |
| Forest Rabbit | common | Sylvilagus brasiliensis |
| Collared Peccary | rare | Tayassu tajacu |
| White-lipped Peccary | not common | Tayassu pecari |
| White-tail deer | common | Odocoileus virginiana |

All local informants insisted that neither brocket deer (Mazama) nor tapirs (Tapirus) have ever been taken in the entire area. Most hunters are familiar with the tapir and correctly indicated where it is to be found in Panama.

Soil samples taken from under forest cover and in recently cleared land (estimated at two years) were analyzed giving the following results:

| | Forest | Pasture |
|---|---|---|
| pH | 6.6 | 6.8 |
| Nitrogen | 50 lbs./acre | 33 lbs./acre |
| Phosphorus | 204 lbs./acre | 204 lbs./acre |
| Potasium | 125 lbs./acre | 103 lbs./acre |
| Calcium | 583 lbs./acre | 583 lbs./acre |
| Organic matter | 10.2% by volume | 4.6% by volume |

Human Influences on the Zoogeography. Tree removal, the rapid and extensive creation of new and permanent pastures and excessive exploitation of game animal populations have resulted in making the major portion of this three province region one of great zoological poverty.

Until approximately 40 years ago, game animals as well as other animal taxa were common to abundant components of a generally forested or heavily wooded area that began east of Nata and extended southwestward into Herrera Province joining with the then much more extensive hill and highland forests of the west-central Azuero Peninsula. In the lower flood plain of the Rio Santa Maria the tree cover was virtually continuous and contained a large component of evergreen species although the formation was probably semi-deciduous. The coming of improvements in the cattle industry led to a direct attack upon this tree cover and radically altered the faunal picture for a large area. In the area of former tree cover the following game mammals and birds are said to have occurred although the present status of each taxon mentioned is often very different than four decades ago:

Mammals

| | | 40-50 years ago | Today |
|---|---|---|---|
| Virginia Oppossum | Didelphis marsupialis | common | common |
| Nine-banded Armadillo | Dasypus novemcinctus | common | uncommon |
| White-face Monkey | Cebus capucinus | common | absent |
| Howler Monkey | Alouatta villosa | common | absent |
| Forest Rabbit | Sylvilagus brasiliensis | uncommon | uncommon |
| Tree Squirrel | Sciurus sp. | common | rare |
| Agouti | Dasyprocta sp. | uncommon | rare |
| Paca | Agouti sp. | uncommon | rare |
| Skunk | Conepatus sp. | common | common |
| Coati-mundi | Nasua narica | abundant | rare |
| Ocelot | Felis pardelis | common | rare |
| Puma | Felis concolor | present | absent |
| Jaguar | Felis onca | present | absent |
| Raccoon | Procyon lotor | common | common |
| Collared Peccary | Tayassu tajacu | abundant | rare |
| White tail Deer | Odocoileus virginiana | abundant | rare |

Birds

| | | | |
|---|---|---|---|
| Wood Quail | Odontophorus sp. | common | common |
| Curassow | Crax sp. | uncommon | absent |
| Little Tinamou | Crypturellus sp. | uncommon | absent |
| Scaled Pigeon | Columba speciosa | seasonally abundant | absent |
| Pale-vented Pigeon | Columba cayennensis | common | rare |
| White-tipped Dove | Leptotila verrauxi | common | abundant |
| Black-bellied Tree Duck | Dendrocygna autumnalis | common | rare |

In the earlier years the very edible and much exploited Iguana, Iguana sp., was extremely abundant but this is now very rare in most of this region. The greatest hunting pressure on this reptile is exerted during the dry season at which time the gravid females are slowed by their burden of eggs. This highly destructive practice has led to the present scarcity of this formerly important rural source of animal protein.

The absence of certain arboreal taxa, especially the two primate genera, formerly present is chiefly the direct result of tree clearing although the last faunal remnents appear to have been deliberately shot without any particular reason. Small bands of howler monkeys, Alouatta, persisted in reduced tree-covered areas along the lower Rio Santa Maria and the lower Rio de La Villa until less than ten years ago but finally gave way to hunters and tree fellers.

The second-growth shrub which was once so common when roza farming dominated much of the land-use (as in aboriginal time) has given way to the rather ecologically sterile conditions of permanent pasture and has grossly reduced the feed and cover conditions required for optimal white-tail deer populations.

As noted repeatedly above in discussions in areas to the west, the open conditions favor the population growth and geographical dispersal of avian taxa chiefly of which the fringillids appear to figure most prominently. The high density of livestock on the plains provides an abundant food supply for vultures whose populations are impressively high especially in comparison with the numbers to be observed in the Tonosi area.

## NORTHWEST PANAMA

The northwest region of Panama is here taken to include the following areas: The Province of Bocas Del Toro and the Atlantic drainage of Veraguas Province.

The western lowland of Bocas Del Toro Province has for many years been devoted to commercial banana production and it is in this area that the most significant recent ecological changes have occurred in the northwest region. The chief banana area is crossed by the Rio Changuinola although lesser areas are given over to the production of this fruit especially in areas to the east around the shores of the Laguna de Chiriqui.

East of the banana lands and up the many small river valleys there are located the numerous but rather isolated settlements of Guaymi Indians. In the immediate vicinity of such settlements there is always a visible amount of forest removal but these areas of disturbance are generally isolated units at present and do not offer continuous corridors for the dispersal of grass or second-growth forms.

East of the narrow peninsula which forms the eastern side of the Laguna de Chiriqui the human population is extremely sparse and there is virtually no evidence of current or recent vegetation disturbance. The heavy unbroken - except by rivers - expanse of forest now covers land that at the time of the first Spanish contact was under fairly heavy cultivation of maize (see Chapter 3.) After the catastrophic reduction of aboriginal populations following upon the conquest period this area appears to have been abandoned and has not been occupied by non-aboriginals except in the most marginal way. This is due in part to the wetter climate as compared with the central plain, the very narrow coastal plain offering but little easily cultivable land and the lack of any sheltered harbor which makes getting ashore during the season of trade winds an exceedingly hazardous task.

With the exception of the banana plantations where human settlement and thus hunting pressures are greatest there is at present little disturbance of the fauna in this region. Most of the region away from the banana lands has not been reported upon in the biological or geographical

literature. Hunters which were interrogated in the area indicated the presence of a fauna that includes virtually all the forest taxa that could be expected to occur in optimal forested conditions in an Am to Af climatic region in this part of the Neotropical region. Interest has recently been expressed elsewhere in Panama for the establishment of hunting camps to which would be attracted North Americans desirous of obtaining game such as jaguars and tapirs both of which are said to be relatively common in the wilder portions of this area.

## CANAL ZONE AND ADJACENT AREAS

The area comprised of Colon Province (excluding the Comarca de San Blas), Panama Province and the Canal Zone may be recognized as another region in Panama, this being united by human population concentrations and, in part, divided by the Canal which so dominates the affairs of this narrow part of the isthmus.

Canal Zone and Associated areas. As noted in Chapter 4, construction of a trans-isthmian ship canal was begun by the French in the 19th century and completed by the U. S. in the 20th century. Detailed accounts of the construction period are easily obtained and the remarks below are written with the assumption that the reader is familiar in a general manner with this aspect of the historical geography of Panama. Thus the remarks to follow focus chiefly upon the influence the canal has had or is having upon the zoogeography of the isthmus.

The canal itself is in many places relatively narrow - just over 100 feet in the individual locks and approximately 150 yards in the long narrow cut south of Gatun Lake.

The canal is spanned by two movable bridges and by one fixed high span bridge. One of the movable bridges form a part of the lock system on the Atlantic side and operates with great frequency every day. The other

movable span is located near the Pacific side of the canal but is not now in operation as its function has been taken over by the high span located a short distance away. The lock doors form narrow bridges each time they are closed which is quite often during the course of each day's operation.

Vegetation disturbance alongside the canal is more or less continuous but some areas, chiefly on the west side, have large tracts of forest close by the water's edge. Vegetation disturbance in the Zone is greatest in the areas of urban, government, and military developments. The greatest area of disturbance occurs on the Pacific side although major disturbance occurs also in Colon. A continuous corridor of grass and second-growth parallels the railroad which is located on the east side of the canal right-of-way.

North of the urban area of Balboa and south of the Chagres River there is a forest preserve crossed by a paved road. This reserve consists of a large stand of semi-deciduous forest in which palms form a conspicuous element. It provides eloquent testimony as to what the vegetation of neighboring areas would be (at least) were there no cutting or burning. A part of the forest preserve boundary coincides with the Canal Zone - Republic of Panama boundary and the phytophysiognomic line here is very sharp with forest on the Zone side and grass and scrubby low second growth on the Panama side - the forest having been removed in recent years by local roza farmers. Few places in Panama offer such an accessible and uncontrovertable illustration of how profound the phytophysiognomic changes have been in recent years due to the human ecological impact upon forested areas.

During World War 2 a surfaced highway was constructed across the isthmus connecting the cities of Panama and Colon for the first time by a reliable all-season automobile and truck route. The road had the effect of

stimulating settlement in an area previously too isolated to attract more than a few persons. Roza farmers invaded the region and have succeeded, in this brief time, in creating a corridor of grass land and second-growth all the way across the isthmus. Up to 1963 the area of greatest changes occurred south of the place where the highway crosses the Changres River, that is, in the Province of Panama. The area of chief present pioneer settlement and, therefore, forest removal is in the vicinity of the highway to the north of the Chagres River - highway intersection in Colon Province.

There is no reason to suppose that the process of forest removal in the area crossed by the highway will decrease in the years ahead. Indeed there is reason to believe that the process may increase a little. This will result in a broad coast-to-coast corridor of grass and low second-growth in which forest stands will be rare or entirely absent.

West and east of Colon city there has been recent removal of a forest that was probably re-established after the period of aboriginal depopulation. There is a fairly rapid removal of forest in the western end of Colon Province to the vicinity of the Rio Cocle Del Norte. Forest removal has been advancing upon Portobelo - here again removing what must certainly be forests established after the period of first Spanish contact. Just east of Portobelo there are generally disturbed vegetation conditions although fairly large stands of forest remain.

On the Pacific side, in addition the vegetation removal associated with the urban areas of Panama City and Balboa, there has been tree removal in and around the several military establishments in the area. If it were not for the current and recent cultural activities of man in this area there would be some type of forest in all locations except where the soil becomes to saline near the edge of the Bahia de Panama. Ample evidence to support this assertion can be seen in the forest remnants near Balboa,

Panama City, the military installations and along the highway between the high bridge and the Panama town of Arraijan. In the vicinity of Arraijan there is a very sharp line of vegetation between the Canal Zone where it is in part protected and the Panama side where heavy pressure from roza farmers have turned the land into pasture and scattered palms and low scrubby second-growth.

Zoogeographical Influences. The most obvious question posed by the area of the Canal Zone is does the canal constitute a water barrier to the dispersal of animals across the isthmian land bridge. The answer cannot be a simple yes or no but requires some discussion.

The narrowness of the canal cut south of the Chagres entrance at Gamboa (Gaillard Cut) and the presence of some tree cover on both sides of the canal probably results in little or no interference to the crossing of most if not all avian taxa present in the area nor must there be any particular barrier to those mammalian taxa present which can swim or, in the case of bats, fly. Mammals present in the general area which should be able to cross by swimming include at least the following: white tail deer, Odocoileus virginiana; ocelot, Felis pardalis; puma, Felis concolor; Jaguar, Felis onca; coati-mundi, Nasua narica; tapir, Tapirus bairdi.

Principally arboreal mammals may find such a modest gap as the one described too formidable to pass and among such taxa I include: the primate genera Cebus, Ateles, Alouatta, Saguinus, Aotus; the little arboreal edentate Cyclopes; the tree porcupine, Coendu; and the two sloths, Bradypus and Choloepus (although Bates reported seeing a sloth swimming in the Amazon at a point where the river was 300 yards wide - Bates, 1910)

Any arboreal mammal just listed as well as some of those not listed might be able to disperse across one of the bridge structures mentioned above. No matter how few chances there may be for such dispersal the possibility exists and, therefore, must be accepted as significant. Such

dispersals, if they were to occur, would most likely involve taxa that are nocturnal or crepuscular in habit as a day-light dispersal would be more difficult for rather obvious reasons.

The canal appears, therefore, to be a partial barrier or, rather, impediment to the dispersal of some mammalian taxa but is probably not a completely effective barrier for any mammalian taxon. This conclusion can be extended to include most of the animal taxa present with the probable exception of certain soil fauna which may not be able to pass the water barrier.

Of greater and growing importance as a barrier to dispersals is the ever widening trans-isthmian corridor of grass and second-growth vegetation. This corridor is large enough at present to be influencing potential dispersals of forest-associated animal taxa and within a decade the width of the corridor will likely be such as to effectively separate the forest fauna of Central America from the forest fauna of South America.

The changed vegetation conditions in the vicinity of the Canal have also produced conditions favoring the dispersal of some animals. The white tail deer appears to have followed the railroad route across the Isthmus at a time preceding the construction of the canal (as mentioned in earlier chapters.) This preeminently edge and second growth species has invaded areas to the east and west of Colon on the Atlantic side and if it is not over hunted will continue to follow the spread of the newly increasing agricultural frontier in the region under discussion.

As elsewhere in Panama, seed-eating birds, especially the finches, find the new conditions of grassland and shrub much to their liking. The following list of birds is representative of the taxa to be found in grass and/or second-growth shrub at almost any point along the disturbed corridors in or adjacent to the Canal Zone or the highway route:

| | |
|---|---|
| Rufous-tailed Hummingbird | Amazilia viridifrons |
| Tropical Kingbird | Tyrannus melancholicus |
| Mourning Warbler | Oporornis philadelphia |
| Yellow-crowned Euphonia | Tanagra lutelcapilla |
| Clay-colored Robin | Turdus grayi |
| Plain Wren | Thryothorus modestus |
| Thick-billed Seed Finch | Oryzoborus funereus |
| Variable Seedeater | Sporophila aurita |
| Yellow-bellied Seedeater | Sporophila nigricollis |
| Blue-black Grassquit | Volatinia jacarina |
| Streaked Saltator | Saltator albicollis |
| Green-backed Sparrow | Arremonops conirostris |

The clearing of forest in the Canal Zone has sometimes not been complete in a given area leaving behind small islands of trees and shrubs in which are to be found remnants of the previously more widespread forest fauna. One such example occurs on the top of Ancon Hill in the Canal Zone (very near the Balboa Administration center.) This hill, which appears to be a plug of resistant volcanic material, is topped by a poor tree cover which has been greatly disturbed on its margins and covers only a few hectares of surface. Mammals observed here include the following: whitetail deer, coati-mundi, agouti, tree squirrels, marmosets - all giving evidence that even very small areas of tree cover will provide the ecological requirements for a varied mammalian fauna if the fauna is afforded protection from hunters and tree cutters.

Hunting in the Canal Zone and adjacent areas has resulted in the serious reduction and near extirpation of several game mammal and bird taxa, viz., brocket deer, Mazama; whitetail deer, Odocoilcus; Tapir, Tapirus; collared peccary and white-lipped peccary, Tayassu sp.; agouti, Dasyprocta; paca, Agouti; Curassow, Crax; guan, Penelope.

It is not generally known that there is a considerable trade in game meat in the city of Panama. Most of this meat is sold in the main public market located at the edge of the bay but game meat is also often sold in other markets in this city. A very significant portion of this meat is obtained in the Canal Zone. There is no regulation of this activity in Panama.

In sum, it can be said that the activities of man in the general area of the Canal Zone have resulted in conditions which will seriously influence the future role of the narrow isthmus as a land bridge. Most of the influence appears to be of a negative nature but some animal taxa, particularly avian forms, will expand into the new grasslands and second-growth covered areas.

Province of Panama, west. The Province of Panama is divided by the Canal Zone into two unequal parts. The western part is by far the smaller of the two but is an area of maximum ecological disturbance.

Maximum vegetation alteration has occurred in a zone aligned with the only major paved route in this area (the east-west Inter-American Highway). However, even in relatively isolated situations the hand of man is clearly seen in the new pastures, isolated trees and exotic plant taxa covering the landscape.

Near the extreme southwestern end of this area the climate and vegetation conditions are the same as those described earlier for the poorer portions of the Cocle plains, a set of conditions owing to the same factors of pronounced annual dry seasons, severe edaphic conditions and extreme misuse of the land by the human occupants.

An interesting and illustrative picture of recent vegetation changes is afforded if the road north from the main highway to the crater valley of El Valle is employed as a transect route. As recently as 1958 most of the region traversed by this side road was in heavy brush and shrubs.

This condition extended up to the rim of the caldera where brush gave way to trees. In 1963 conditions were very different and instead of the shrub covered slopes there was an almost unbroken expanse of faragua grass extending up to the caldera rim and in places descending well down toward the floor of the crater. The former lush forest had been cut back to small remnant areas and these were under attack.

Returning to the main highway, the country eastward becomes increasingly moist as compared with the Cocle plains. From Chame eastward the grasslands retain a markedly greener cast during the dry season as compared with dryer parts of the Republic during the same period. All the tree vegetation in the neighborhood of the highway had recently undergone major reduction but it appears that this is another area where forest may have become reestablished in post-conquest time. Espinosa reported on his having ridden by horseback through this area which he characterized as very open (see Chapter 3). Within a decade virtually all forest will have been removed from this zone.

Even relatively steep slopes have not deterred people from cutting down the tree cover. The slopes of Cerro Campana, a volcanic plug (see Chapter 1), would appear much too steep to make them attractive for pasture but nevertheless tree removal has progressed rapidly here so that by 1963 only a small, and rapidly diminishing, forest area remained in the higher parts of this upland. The once tree-clad slopes are in grasses and sedges upon which a few head of livestock seek sustenance.

Zoogeographic Influences. The major apparent influence that man has recently had upon the zoogeography of this area is that of opening a grassland corridor through a forested area which has permitted the dispersal of animal taxa associated with such changed ecological conditions. Reduction of forest cover had had an adverse effect upon forest-associated animal taxa.

The rapid destruction of tree cover at the higher elevations of this area has very serious implications because the summit fauna contains elements that occur only disjunctly at present in the southern part of the Central American isthmus. The small remaining tracts should be given the strongest legal protection.

Hunting pressure in this area has had the effect of reducing the populations of game animals and birds to a point that hunting is no longer regarded as an important means of obtaining food. The destruction of the brushlands mentioned above seems to have had a very negative effect upon whitetail deer numbers but the reduction must be equally due to over exploitation.

Province of Panama, east. The non-urban area of the eastern portion of the Province of Panama will be most easily described it the area is divided into four sub-regions, viz., (1) highlands east of Madden Lake, (2) east edge of Panama City to El Llano on the Rio Bayano, (3) the Rio Bayano valley, (4) the serrania de Maje (or de Canazas.)

(1) The highlands east of Madden Lake constitute one of the wildest and least known areas of Panama. Heavily clothed in forest and very difficult of access, this tabular upland has not received other than peripheral ecological disturbances by man in the modern period and it may be that this area has never been much influenced by human activity though such a conclusion must await archaeolgical investigations.

(2) The lowland zone extending between Panama City and El Llano on the Rio Bayano is an area in which it appears that human activities have been the cause of much of the very obvious ecological disturbance. Much of the ecological changes must have occurred during the pre-conquest period but since this region was occupied b the Spanish early in the sixteenth century there has been a long and essentially unbroken cultural - ecological history of impoverishment of vegetation, soils, and fauna.

A paved road extends across this lowland from Panama City to Chepo after which the route becomes an unpaved dry season tract to El Llano. Throughout the length of this transect the vegetation shows major signs of having been maximally disturbed as a result of cultural activities.

Just east of the last of the urban development near Panama City the land (1963) was in pasture - faragua, para, guinea, and other exotic grasses - and in tracts of second-growth shrub in which Cecropia spp. is a very conspicuous element. In somewhat older stands of second-growth forms such as Barrigon, Bombax, or Cuipo, Cavanillesia platanifolia, are often very conspicuous. It is desired that note be taken here that the Cuipo appears to be a taxon that is associated with disturbed ecological conditions and when it occurs in lowland situations is almost certain to indicate by its presence that it is part of a seral stage that is not the "climax". Cuipo is often encountered on very steep slopes and ridge tops where it may be expected that edaphic conditions are continuously unstable. It appears to invade lowland areas from these upper positions when the lowland vegetation has been disturbed by roza farming and similar activities.

With increasing distance eastward the dry season character of the vegetation changes to more vivid greens and that indicator of soil moisture Heliconia spp., becomes abundant in recently abandoned roza tracts or alongside the road way. The increased moisture supports roadside stands of espave, Anacardium excelsum, and higueron, Ficus spp., but most of the land is in permanent pasture. In dryer portions of this zone chumico, Curatella americana, nance, Byrsonima crassifolia, and maranon, Anacardium occidentale, are common to abundant.

(3) The middle and upper parts of the Rio Bayano valley are inhabited by the Bayano Cuna Indians - remnant of a once far more numerous group that at the time of Spanish conquest occupied almost all of the eastern two-thirds of Panama. The present-day ecology of this group has recently been

reported upon (Bennett, 1962).

These Indians depend upon their own agricultural and hunting and fishing activities to provide their required food.

Shifting cultivation (roza) is the type of agriculture employed with the chief food crops being, in order of importance, bananas, plantains, and maize. In spite of a recent statement to the contrary (Ladd, 1964) manioc, Manihot, or other tubers are not here nor elsewhere in eastern Panama presently of any particular dietary importance though they are cultivated.

Areas given over to cultivation are often scattered in a random fashion over the land but are usually close to a stream or are located adjacent to village sites. In the latter case the arrangement of the land under agriculture use tends to be orderly. This near-the-settlement-cultivation consists of small gardens next to the owners house (Bennett, 1965) and of plots distributed near well-established footpaths. The arrangement of farm plots between the villages of Icandi and Pintupo is shown in Map 9. It should be noted how very mixed is the phytophysiognomy and the varied animal habitats which are created by such a system of land practice. Of course, at present the areas of farmed land are small and are disjunctly located. A greater number of Cuna, though, would be able to extend the conditions shown on Map 9 over large areas - a point to keep in mind when trying to reconstruct pre-historical ecological conditions in this region.

At present, forest covers the greater part of the middle and upper Rio Bayano area. The relative abundance of cuipo trees in the region suggests that much of the present forest cover has reappeared in post-contact time. This would seem to accord with the accounts of the first Spanish entradas into the area.

(4) The Serrania de Maje region is an isolated and almost unknown part of the isthmus of Panama. The slopes are now under heavy forest cover and this was apparently the condition when the Spanish arrived. An air reconnaissance of the summit region indicated that cuipo is common on some of the sharper ridges. The area is only occasionally penetrated by hunters and there were no evidences of permanent human occupance except at the base of this small range.

Zoogeographic Influences. The most pronounced recent human influences on the zoogeography of eastern Panama Province have occurred in the zone between Panama City and El Llano. This has been due to forest removal per se and to extreme hunting pressure. Market hunting is done in this zone but little success attends such efforts until the area east of Chepo is reached.

Ecological disturbance in the Bayano area is not now sufficient to influence the faunal picture to any appreciable extent. Although the Cuna are avid hunters their numbers are too few to result in overexploitation except in some extremely local instances. Game mammals such as brocket deer, Mazama, and tapirs, Tapirus, are still numerous in the Cuna lands as are also the other bird and mammals which they hunt.

Although grassland conditions have been extended to El Llano, beyond this point strictly grassland taxa cannot now easily disperse. However, a highway is being planned that will connect Panama with Colombia and if this should come into being there will result in the kind of corridor that grass and second growth conditions which have been described repeatedly above for other parts of Panama. The highway will attract a horde of roza farmers from elsewhere in Panama and the ecological outcome is only too clear.

## EASTERN PANAMA

The region here designated as EASTERN PANAMA includes the Province of

Darien and the Comarca de San Blas.

Darien Province. The human population of Darien is racially heterogeneous but economically rather uniform. Two aboriginal groups occur here, in the Choco and Cuna, of which the former is by far the larger group. A large Negro population is concentrated in and around the major settlements of the province.

The chief economic activity is that of shifting cultivation. There is also a significant amount of cash crop agriculture - chiefly bananas and plantains - but this activity is concentrated in the lower parts of the Rio Chucunaque and Rio Tuira valleys. It is in this last area that recent vegetation disturbance has been greatest.

Other areas of recent and ecologically significant amounts of vegetation removal include the valley of the Rio Sambu, the valley of the Rio Tucuti, the area adjacent to Jaque, and the shores of the Golfo de San Miguel - especially between Garachine and La Palma.

All the areas of maximum plant disturbance are characterized by grassy expanses and frequent tracts of low second-growth shrub or trees. Perhaps the most intensively disturbed area is to be found along the Rio Chico in the lower Chucunaque valley. In this culturally mixed area of Choco and Negroes the land is given over to commercial and subsistence agriculture which has led to a major reduction or elimination of forest cover.

However, most of the Province of Darien is presently under forest cover which in the lowlands along the Chucunaque is dominated by one tree species, the cuipo, Cavanillesia platanifolia. In view of the land use and settlement at the time of first European contact in this area it may be suggested that the present forest has largely been re-established since the sixteenth century and is still passing through a series of seral stages presently marked by the dominance of the cuipo, a softwood species.

Zoogeographic Influences. The influence of current and recent human populations of the fauna of Darien is and has been limited to areas adjacent to the settled parts of the province. In some of these areas, especially in the Sambu area and in the Rio Chico - Yaviza area, virtually all the larger game mammals and birds have been extirpated locally. Away from these areas of over exploitation animal populations must at present be little influenced by the human presence.

Allusion was made above to a planned highway through this region and it should be stated again that should such a highway materialize there will result a corridor of disturbed vegetation through this extensive forest region which presently must act as a significant barrier to the dispersal of grass and open land animal taxa presently occurring on both sides of the barrier.

Of even greater potential zoogeographic significance would be the construction of a sea-level canal in the Darien region. Such a canal would very likely form a major barrier to the further dispersal of virtually all but volant animal taxa between Central and South America.

Comarca de San Blas. Stout (1947) has reported upon some of the aspects of the San Blas Cuna Indians who constitute almost the sole cultural unit inhabiting the Comarca de San Blas. The Cuna engage in shifting cultivation and some sedentary cash crop agriculture (coconuts, Cocos nucifera) in combination with marine subsistence fishing and a very minor amount of livestock husbandry.

The lands utilized for agriculture lie in a narrow belt between the Serrania del Darien and the Caribbean Sea. There is presently a continuous zone of vegetation disturbance throughout the farmed part of the Comarca which links similar areas in neighboring Colombia with the entire complex of grass and second-growth described for other parts of Panama. Thus it

appears that it is now possible for some edge and second-growth animal taxa to disperse between South America and Central America. There probably is not yet sufficient development of grassland to permit the dispersal of most of the fringillids mentioned in other parts of Panama.

Although the San Blas Cuna population appears to be approximately stable only slight increases in the future should serve to effect a more open corridor through which a large number of animal taxa might possibly move or meet.

There is still a continuous belt of forest in the Serrania del Darien and thus it may be presumed that there is little faunal disturbance here.

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Table 1. - Distribution of Mammalian Genera which Occur in the Central American Province of the Brazilian Subregion.

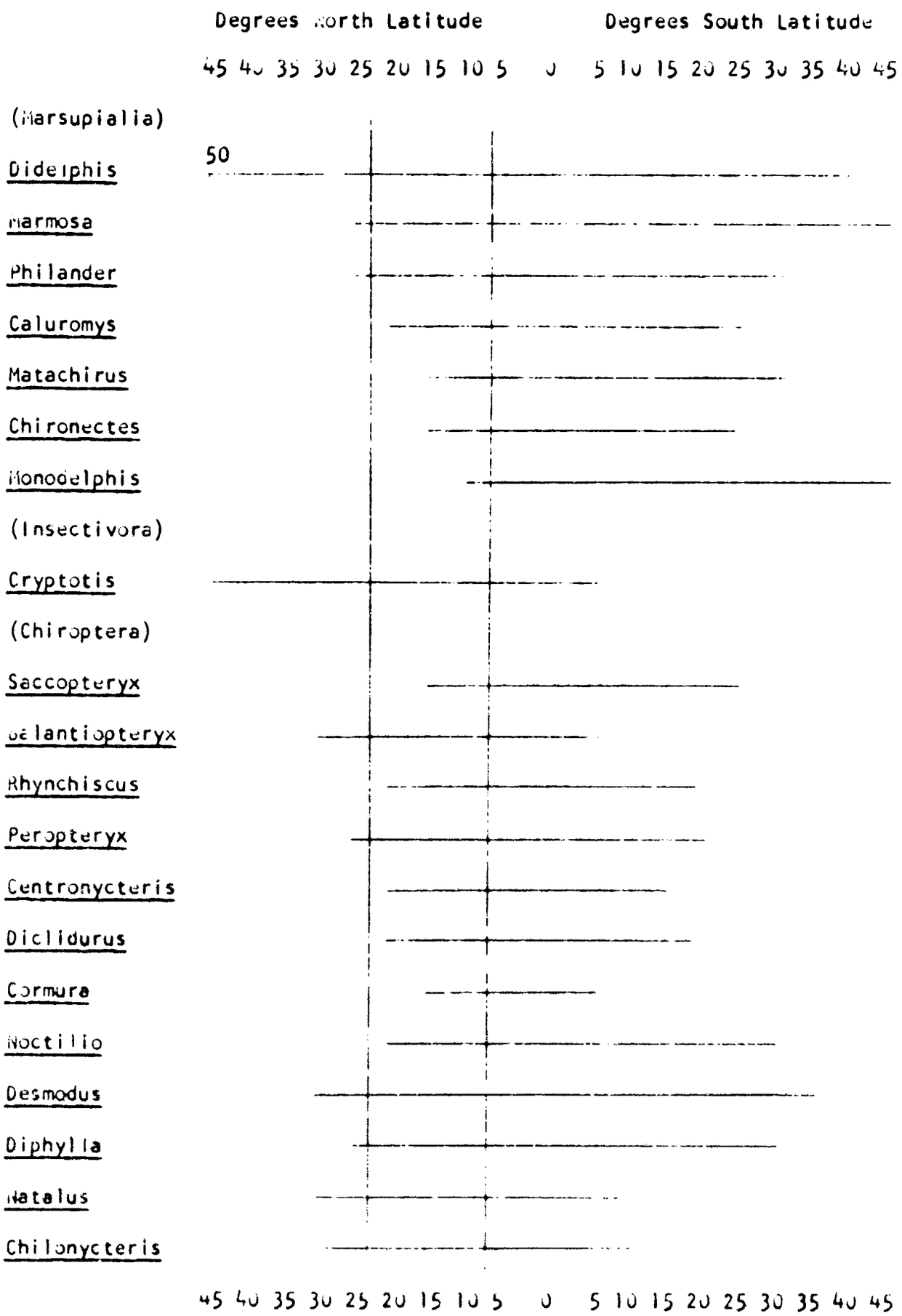


Table 1. (Cont.)

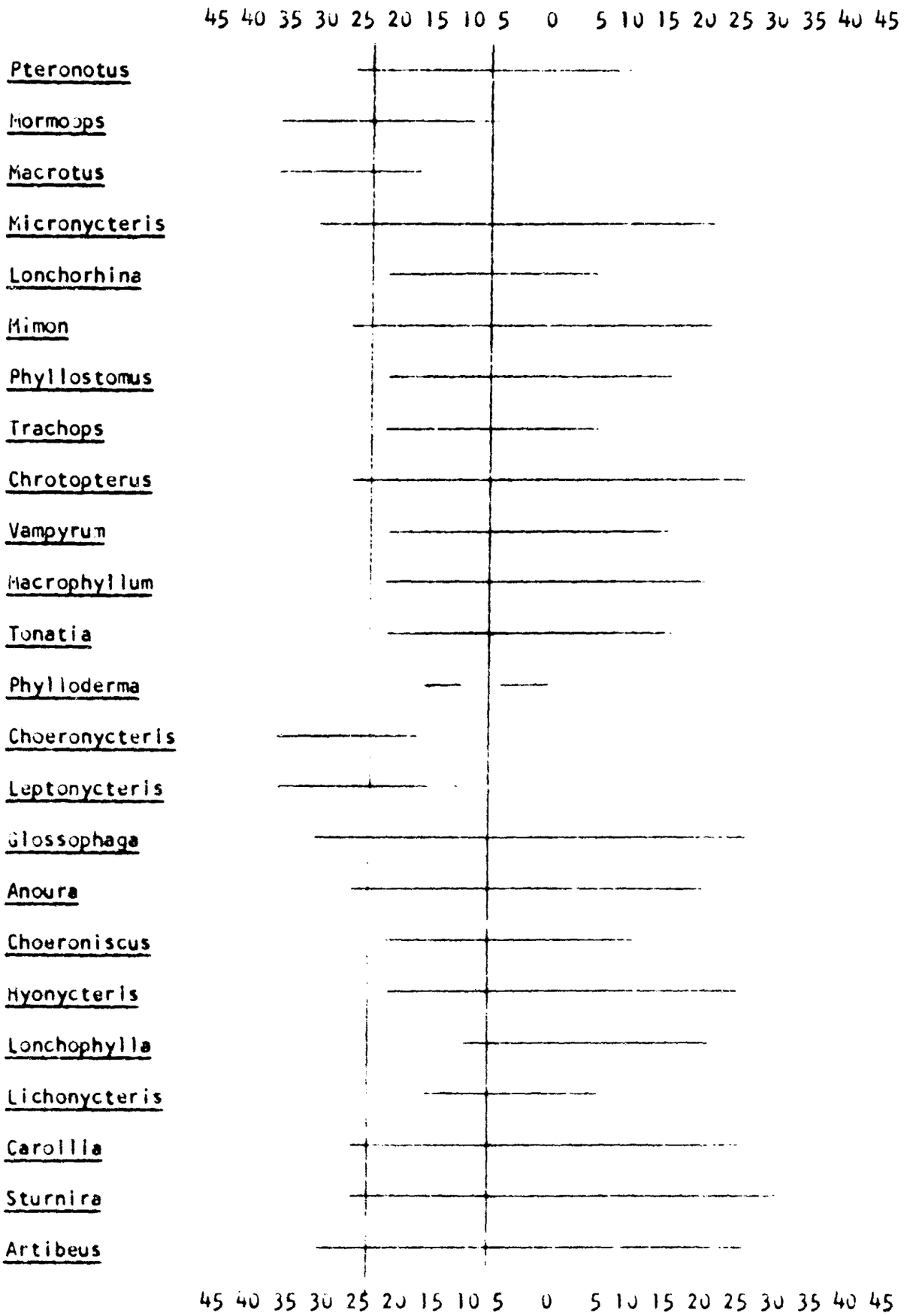

45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45
Pteronotus
Mormoops
Macrotus
Micronycteris
Lonchorhina
Mimon
Phyllostomus
Trachops
Chrotopterus
Vampyrum
Macrophyllum
Tonatia
Phylloderma
Choeronycteris
Leptonycteris
Glossophaga
Anoura
Choeroniscus
Hyonycteris
Lonchophylla
Lichonycteris
Carollia
Sturnira
Artibeus
45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45

Table 1. (Cont.)

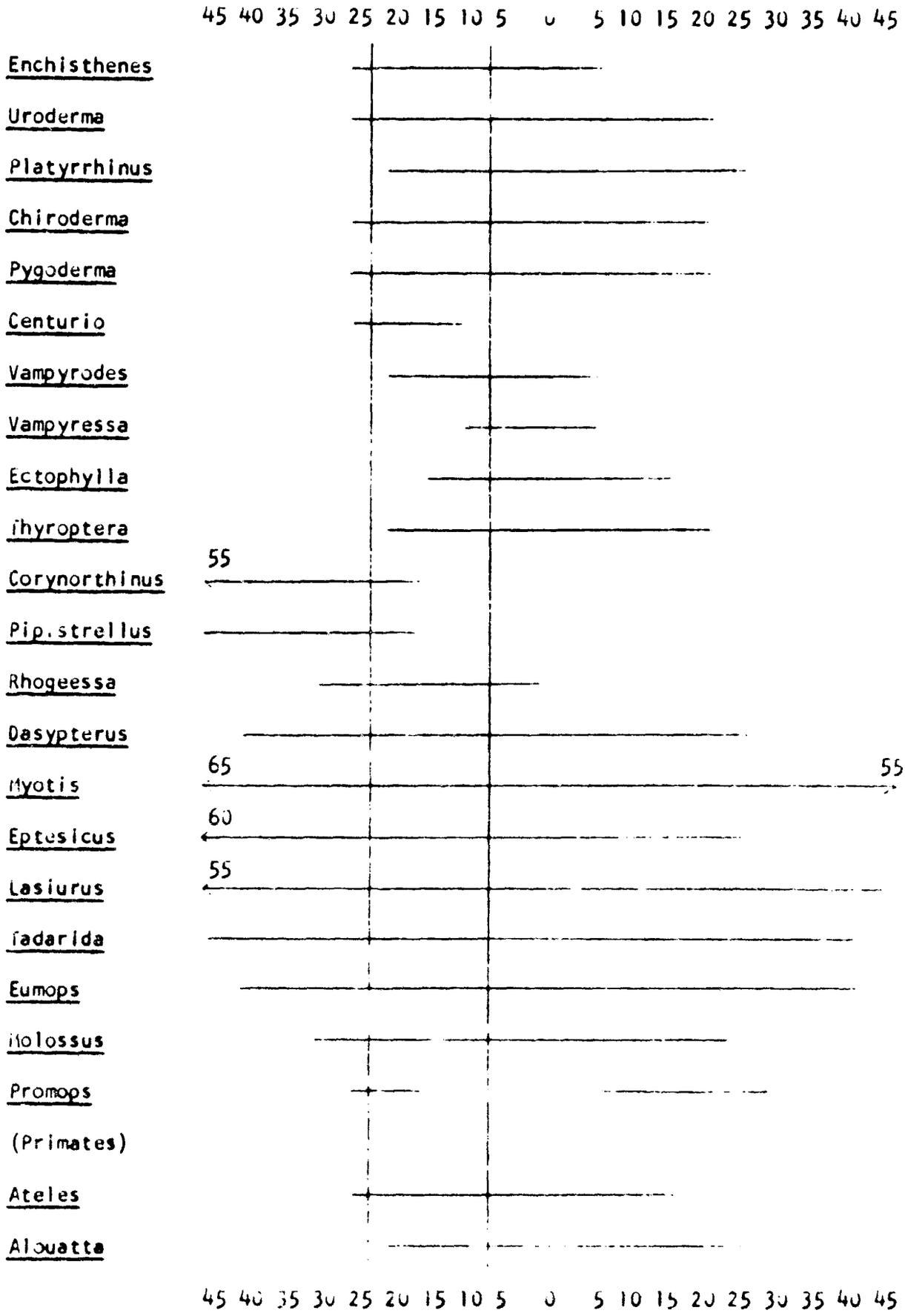

45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45
Enchisthenes
Uroderma
Platyrrhinus
Chiroderma
Pygoderma
Centurio
Vampyrodes
Vampyressa
Ectophylla
Thyroptera
55
Corynorthinus
Pip.strellus
Rhogeessa
Dasypterus
65
55
Myotis
60
Eptesicus
55
Lasiurus
Tadarida
Eumops
Molossus
Promops
(Primates)
Ateles
Alouatta
45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45

Table 1. (Cont.)

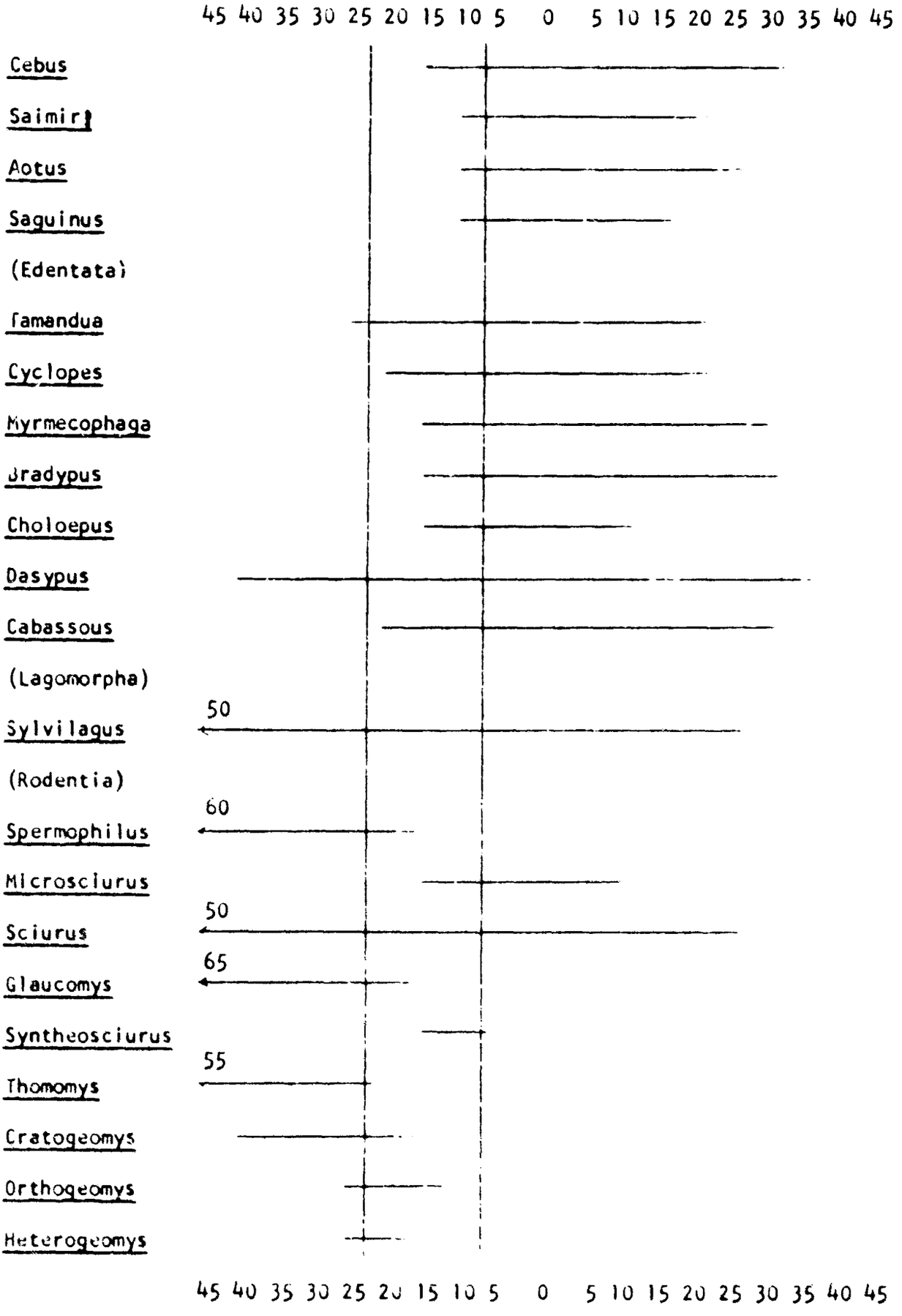

45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45
Cebus
Saimiri
Aotus
Saguinus
(Edentata)
Tamandua
Cyclopes
Myrmecophaga
Bradypus
Choloepus
Dasypus
Cabassous
(Lagomorpha)
50
Sylvilagus
(Rodentia)
60
Spermophilus
Microsciurus
50
Sciurus
65
Glaucomys
Syntheosciurus
55
Thomomys
Cratogeomys
Orthogeomys
Heterogeomys
45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45

Table 1. (Cont.)

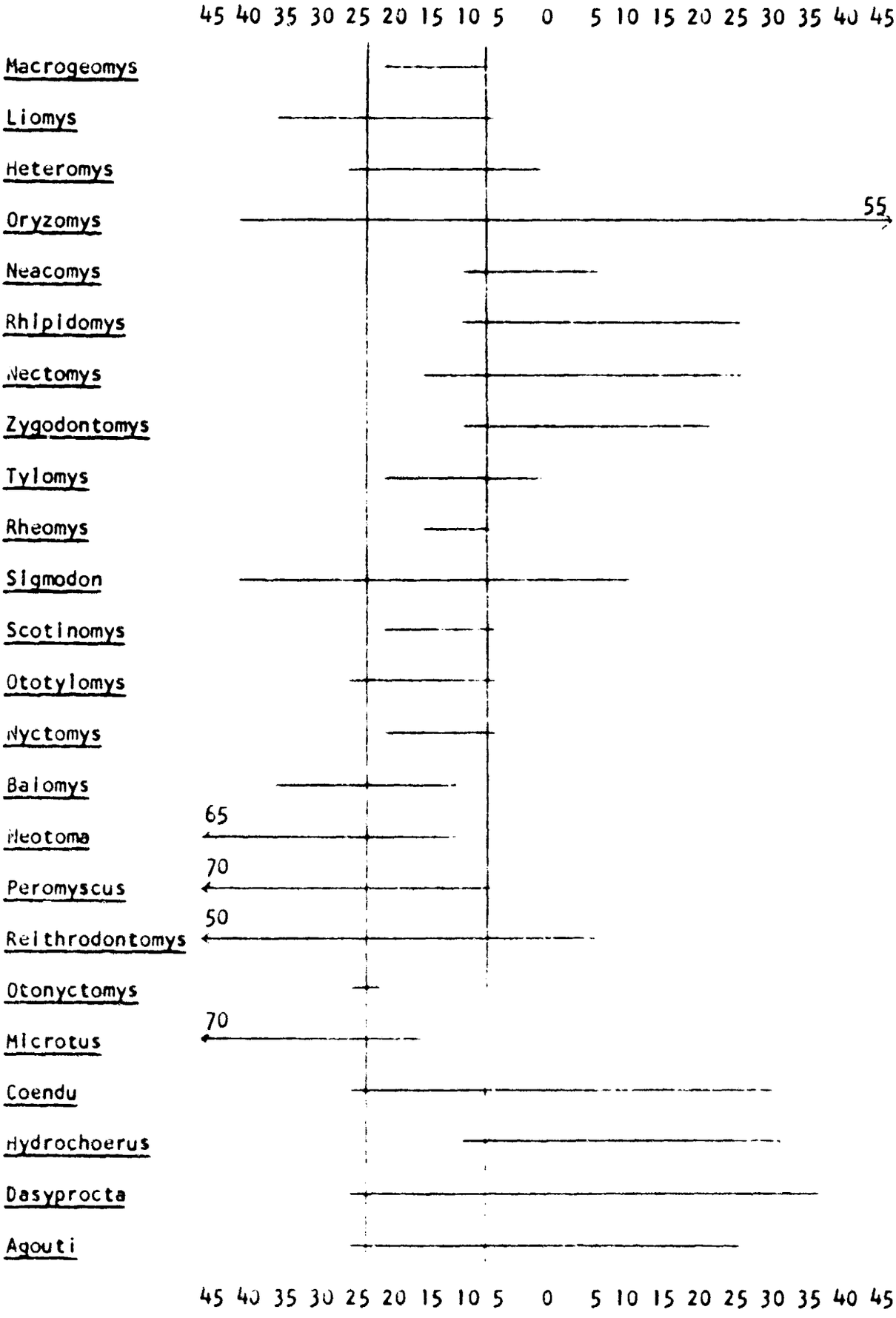

45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45
Macrogeomys
Liomys
Heteromys
Oryzomys
55
Neacomys
Rhipidomys
Nectomys
Zygodontomys
Tylomys
Rheomys
Sigmodon
Scotinomys
Ototylomys
Nyctomys
Baiomys
65
Neotoma
70
Peromyscus
50
Reithrodontomys
Otonyctomys
70
Microtus
Coendu
Hydrochoerus
Dasyprocta
Agouti
45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45

Table 1. (Cont.)

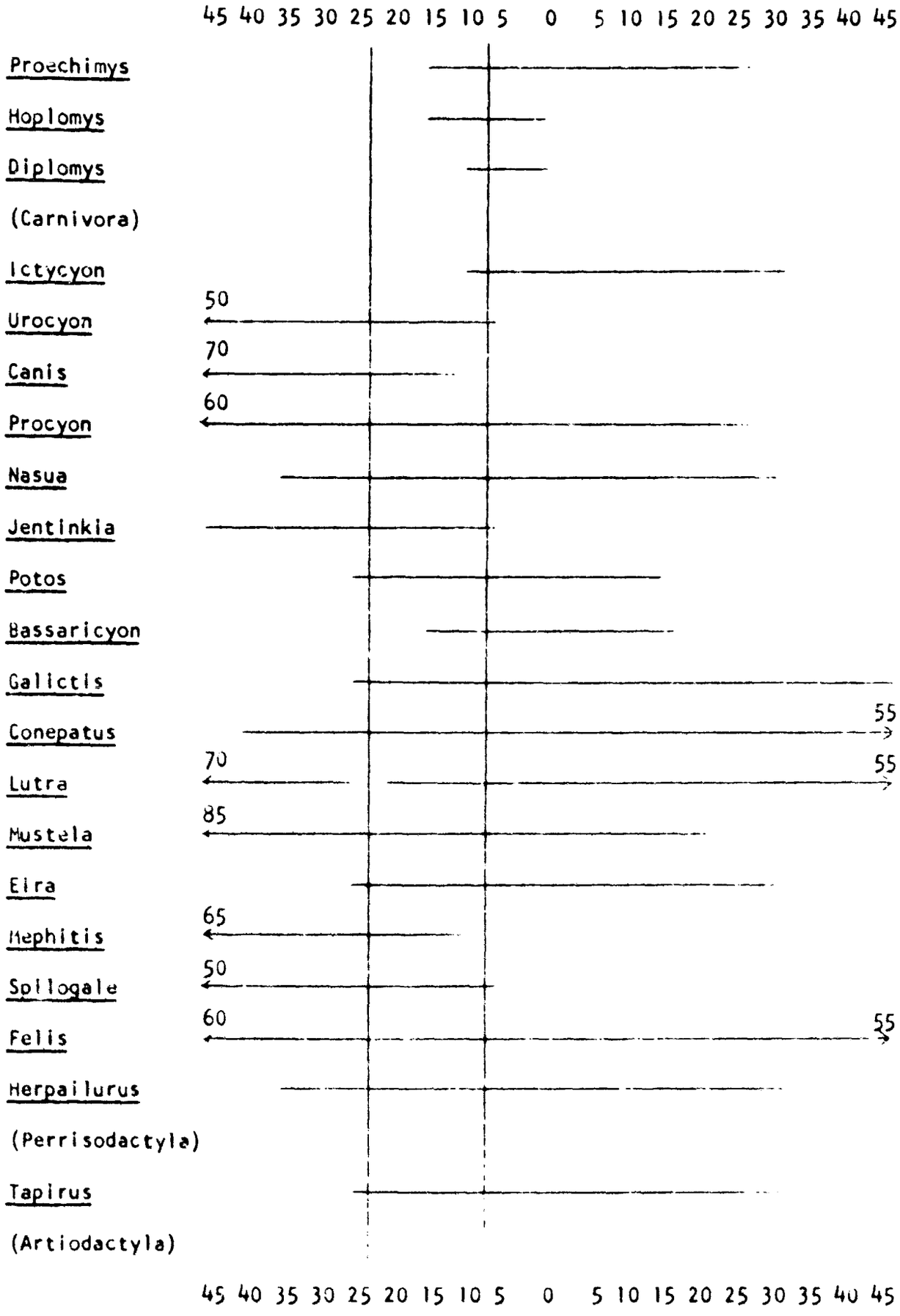
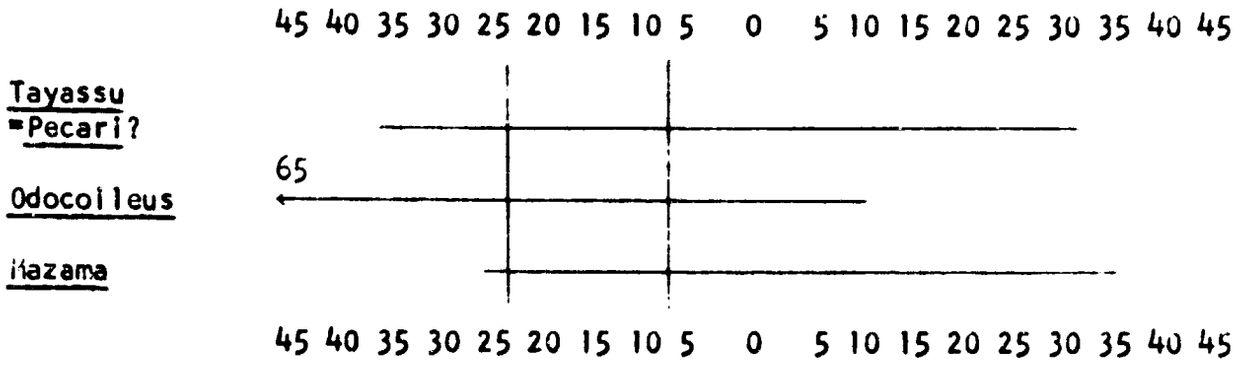

45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45
Proechimys
Hoplomys
Diplomys
(Carnivora)
Ictycyon
Urocyon
50
Canis
70
Procyon
60
Nasua
Jentinkia
Potos
Bassaricyon
Galictis
Conepatus
55
Lutra
70
55
Mustela
85
Eira
Mephitis
65
Spilogale
50
Felis
60
55
Herpailurus
(Perrisodactyla)
Tapirus
(Artiodactyla)
45 40 35 30 25 20 15 10 5 0 5 10 15 20 25 30 35 40 45

Table 1. (Cont.)

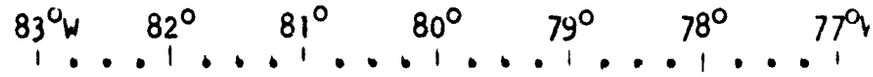



The vertical lines delimit the area between 7°N and 23°30'N, i.e., Central America and the Mexican portion of the Neotropical Region.

Sources: Cabrera, 1957, 1960; Hall and Kelson, 1959; Hershkovitz, 1958; Miller and Kellogg, 1955.

Table 2. Distribution of Some Mammalian Species which Occur in Panama

(Provisional)




(Marsupialia)

Didelphis marsupialis

Chironectes panamensis

Philander opossum

Marmosa mexicana

Marmosa invicta

Caluromys derbianus

Monodelphis melanops

Metachirus nudicaudatus

(Insectivora)

Cryptotis endersi

Cryptotis zeteki

Cryptotis tersus

Cryptotis mera

(Primates)

Aotus bipunctatus (1)

Aotus trivirgatus

Alouatta villosa

Cebus capucinus

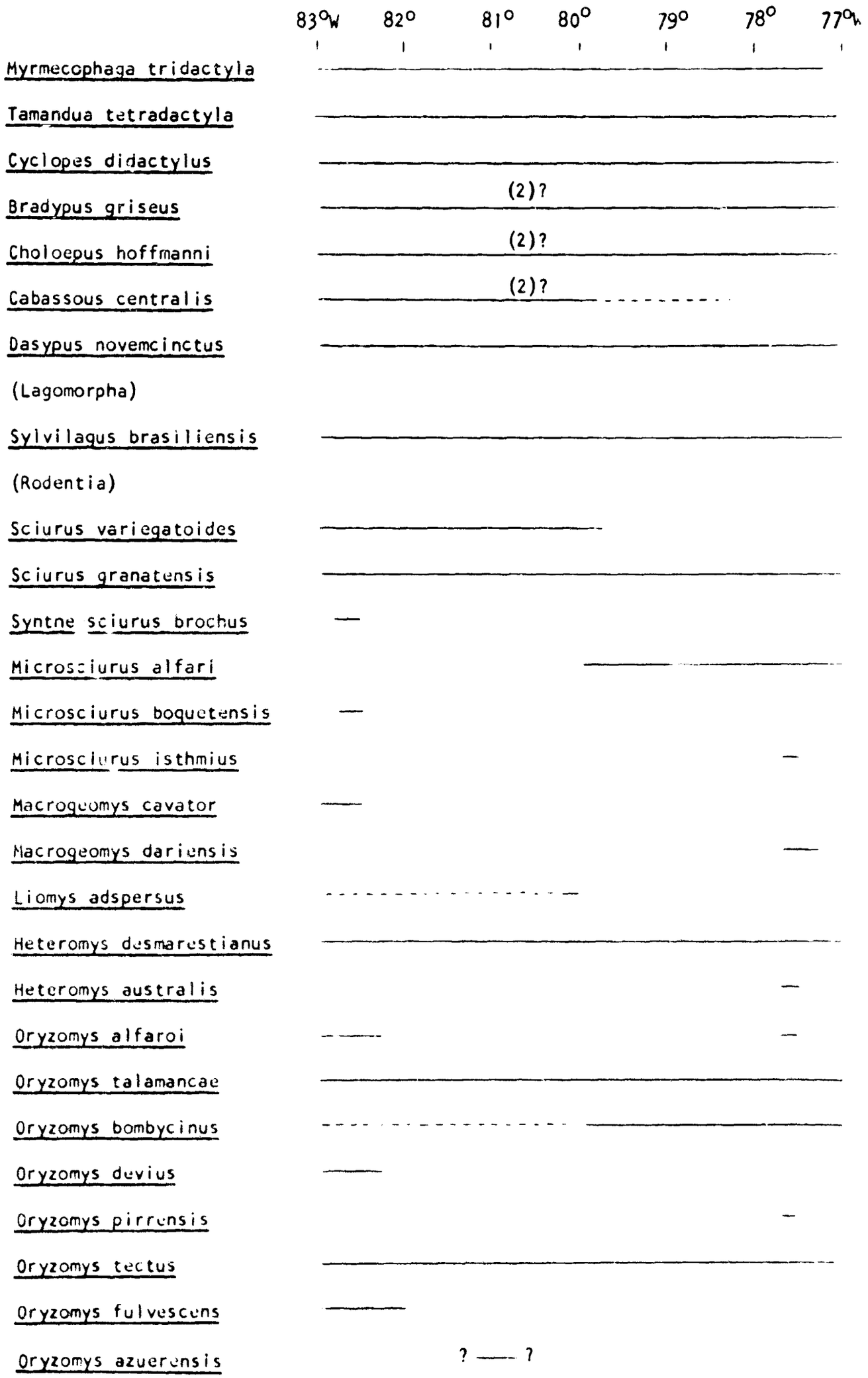
Saimiri orstedii

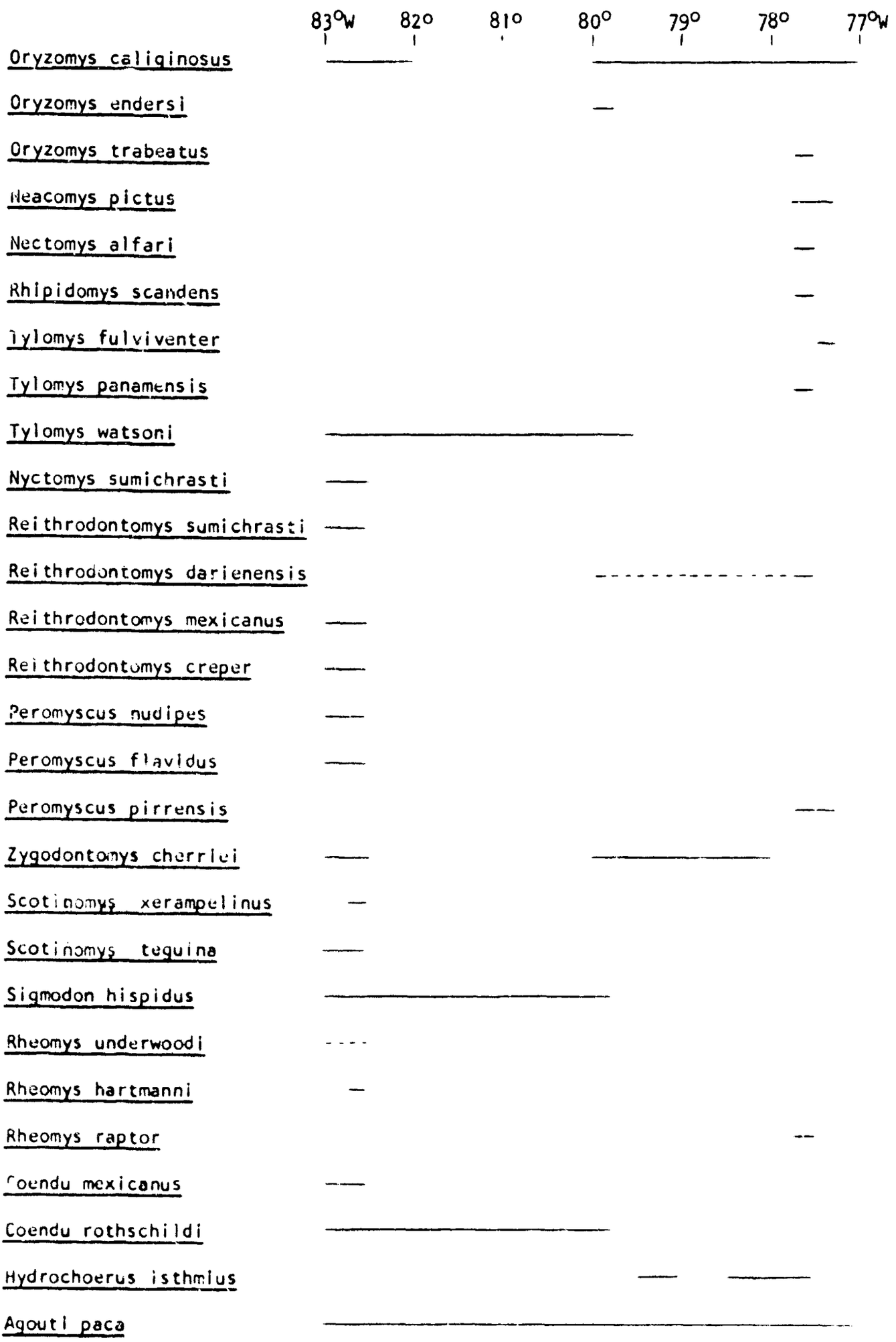
Ateles geoffroyi

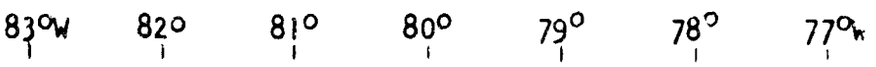
Ateles fusciceps

Saguinus geoffroyi (2)

(Edentata)


83°W
82°
81°
80°
79°
78°
77°
Myrmecophaga tridactyla
Tamandua tetradactyla
Cyclopes didactylus
Bradypus griseus
(2)?
Choloepus hoffmanni
(2)?
Cabassous centralis
(2)?
Dasypus novemcinctus
(Lagomorpha)
Sylvilagus brasiliensis
(Rodentia)
Sciurus variegatoides
Sciurus granatensis
Syntne sciurus brochus
Microsciurus alfari
Microsciurus boquetensis
Microsciurus isthmius
Macrogeomys cavator
Macrogeomys dariensis
Liomys adspersus
Heteromys desmarestianus
Heteromys australis
Oryzomys alfaroi
Oryzomys talamancae
Oryzomys bombycinus
Oryzomys devius
Oryzomys pirrensis
Oryzomys tectus
Oryzomys fulvescens
Oryzomys azuerensis
? ? ?


83°W
82°
81°
80°
79°
78°
77°W
Oryzomys caliginosus
Oryzomys endersi
Oryzomys trabeatus
Neacomys pictus
Nectomys alfari
Rhipidomys scandens
Tylomys fulviventer
Tylomys panamensis
Tylomys watsoni
Nyctomys sumichrasti
Reithrodontomys sumichrasti
Reithrodontomys darienensis
Reithrodontomys mexicanus
Reithrodontomys creper
Peromyscus nudipes
Peromyscus flavidus
Peromyscus pirrensis
Zygodontomys cherriei
Scotinomys xerampelinus
Scotinomys teguina
Sigmodon hispidus
Rheomys underwoodi
Rheomys hartmanni
Rheomys raptor
Coendu mexicanus
Coendu rothschildi
Hydrochoerus isthmius
Agouti paca




Dasyprocta punctata

Hopolomys gymnurus

Proechimys semispinosus

Diplomys darlingi

(Carnivora)

Urocyon cinereoargenteus

Speothos panamensis

Jentinkia sumichrasti

Procyon lotor

Procyon cancrivorus (2)?

Nasua narica

Potos flavus

Bassaricyon gabbii

Bassaricyon pauli

Mustela frenata

Eira barbara

Galictis allamandi

Conepatus semistriatus

Lutra annectens

Felis onca

Felis concolor

Felis pardalis

Felis wiedii

Herpailurus yagouaroundi

(Perissodactyla)

Tapirus bairdii (2)

(Artiodactyla)

Tayassu tajacu

| | 83°W | 82° | 81° | 80° | 79° | 78° | 77°W |
|---|---|---|---|---|---|---|---|
| Tayassu pecari | ——— | | | | | | |
| Odocoileus virginiana | ——— | | | | | — | |
| Mazama americana | | | | (2) | | | ——— |

Symbols employed in Table 2:

(1) Known only from the Azuero Peninsula

(2) Not known from the Azuero Peninsula

---- Doubtful range.

Sources: Aldrich and Bole, 1937; Galindo, 1963 (pers. comm.); Goldman, 1920; Hall and Kelson, 1959; Hershkovitz, 1958; Miller and Kellogg, 1955.

Comments: It appears from the table that there are at least four distinct mammalian distributional patterns on the Panamanian isthmus, viz.,

(1) Distributions restricted largely to the highlands of western and/or eastern Panama, e.g., Cryptotis, Microsciurus, Reithrodontomys, Peromyscus.

(2) An eastern Panama pattern with the western boundary being near the Canal Zone, e.g., Metachirus, Hoplomys, Hydrochoerus.

(3) A western Panama pattern with the eastern boundary occurring near the Canal Zone, e.g., Cabassous, Sigmodon, Procyon lotor.

(4) An absence of certain expected taxa in the Azuero Peninsula area, e.g., Mazama, Tapirus, Saguinus.

To some degree (perhaps very importantly in many cases) the distributions shown in this table reflect the distribution of the collecting efforts of biologists over the years. This is particularly true of the central sierra east of the El Baru region, west central Panama, the south two-thirds of the Azuero Peninsula, the Serrania de Majé, and the Atlantic coast between the Canal and Almirante Bay.

TABLE 3

MAMMALS[1] FROM ISLANDS IN THE TERRITORIAL WATERS OF PANAMA

Islands Immediately South of David

| | |
|---|---|
| Virginia Opossum | Didelphis marsupialis |
| Wooly Opossum | Caluromys derbianus |
| Brown Opossum | Metachirus nudicaudatus |
| Howler Monkey | Alouatta villosa |
| Squirrel Monkey | Saimiri oerstedii |
| Two-toed Sloth | Cholocpus hoffmanni |
| Tree Squirrel | Sciurus sp. |
| Tree Porcupine | Coendou rothschildi |
| Spiny Rat | Proechimys sp. |
| Kinkajou | Potos flavus |

Islas Cebaco and Gobernador

| | |
|---|---|
| Virginia Opossum | Didelphis marsupialis |
| Wooly Opossum | Caluromys derbianus |
| Two-toed Sloth | Choloepus hoffmanni |
| Tamandua | Tamandua tetradactyla |
| Forest Rabbit | Sylvilagus brasilensis |
| Tree Squirrel | Sciurus sp. |
| Hispid Cotton Rat | Sigmodon hispidus |
| Harvest Mouse | Reithrodontomys sp. |
| Cane Rat | Zygodontomys cherriei |
| Spiny Rat | Proechimys sp. |

Isla Coiba

| | |
|---|---|
| Virginia Opossum | Didelphis marsupialis |
| Howler Monkey | Alouatta villosa |
| White-face Monkey | Cebus capucinus |
| Agouti | Dasyprocta sp. |
| Whitetail Deer | Odocoileus virginiana |

Isla San Jose

| | |
|---|---|
| Agouti | Dasyprocta punctata |
| Spiny Rat | Proechimys semispinosus |
| Brocket Deer | Mazama gouazoubira |

Isla del Rey

| | |
|---|---|
| Virginia Opossum | Didelphis marsupialis |
| House Opossum | Marmosa mitis |
| Forest Rabbit | Sylvilagus brasiliensis |
| Cane Rat | Zygodontomys scorsus |
| Agouti | Dasyprocta punctata |
| Spiny Rat | Procchimys spinosus |
| Gliding Spiny Rat | Dipicmys labilis |

Isla Escudo De Veragua

| | |
|---|---|
| Thick-spined Rat | Hoplomys gymnurus |

(1) Excludes Bats.

TABLE 4

HUMAN POPULATION OF PANAMA, 1911, 1920, 1930, 1940, 1950, 1960
(By Province)

| Year | Republic of Panama | Bocas Del Toro | Coclé | Colón | Chiriquí | Darién | Herrera | Los Santos | Panama | Veraguas |
|---|---|---|---|---|---|---|---|---|---|---|
| 1911 | 336,742 | 22,732 | 35,011 | 32,092 | 63,364 | 8,992 | 23,007 | 30,075 | 61,855 | 59,614 |
| 1920 | 446,098 | 27,239 | 45,151 | 58,250 | 76,470 | 10,728 | 28,984 | 34,638 | 98,035 | 66,603 |
| 1930 | 467,459 | 15,851 | 48,244 | 57,161 | 76,918 | 13,391 | 31,030 | 41,218 | 114,103 | 69,543 |
| 1940 | 622,576 | 16,523 | 55,737 | 78,119 | 111,206 | 14,930 | 38,118 | 49,621 | 173,328 | 84,994 |
| 1950 | 805,285 | 22,392 | 73,103 | 90,114 | 138,136 | 14,660 | 50,095 | 61,422 | 248,355 | 106,998 |
| 1960 | 1,067,766 | 32,110 | 93,406 | 103,738 | 186,801 | 19,594 | 61,531 | 70,372 | 369,280 | 130,934 |
| Inhabitants per sq. mi. | | | | | | | | | | |
| 1960 | | 9.5 | 47.8 | 36.6 | 55.7 | 3.0 | 65.8 | 47.2 | 81.6 | 30.7 |
| 1911 | | 6.6 | 18.0 | 11.3 | 18.7 | 1.4 | 24.5 | 20.1 | 13.6 | 13.9 |

Source: República de Panamá. Dirección de Estadistica y Censo (1961).

TABLE 5

AMERIND POPULATION IN PANAMA, 1930, 1940, 1950, 1960
(By Province)

| Year | Republic Total | Bocas Del Toro (1) | Coclé (1) | Colón (2) | Chiriquí (1) | Darién (3) | Herrera (1) | Los Santos (1) | Panama (4) | Veraguas (1) |
|---|---|---|---|---|---|---|---|---|---|---|
| 1930 | 42,897 | 5,103 | 3,459 | 15,154 | 9,851 | 6,809 | 30 | 3 | 1,281 | 1,207 |
| 1940 | 55,987 | 6,574 | 0 | 20,822 | 19,135 | 6,651 | 0 | 0 | 1,329 | 1,476 |
| 1950 | 48,654 | 9,147 | 0 | 17,350 | 14,238 | 4,180 | 0 | 0 | 1,691 | 1,998 |
| 1960 | 62,187 | 12,629 | 0 | 19,343 | 19,946 | 5,777 | 0 | 0 | 1,200 | 3,292 |

(1) Guaymí
(2) San Blas Cuna
(3) At least 90% Chocó
(4) At least 30% River Cuna

Sources: República de Panamá. Censos de 1950; Censos de 1960. (And field reconnassance)

TABLE 6

AMERIND SETTLEMENT SIZE, PANAMA, 1960

| Inhabitants per settlement | Guaymí | San Blas Cuna | River Cuna | Chocó |
|---|---|---|---|---|
| 1-9 | 182 | 12 | 3 | 41 |
| 10-19 | 207 | 9 | 1 | 38 |
| 20-29 | 166 | 6 | 1 | 5 |
| 30-39 | 98 | 3 | - | 5 |
| 40-49 | 61 | 4 | - | 8 |
| 50-99 | 136 | 5 | 4 | 6 |
| 100-199 | 45 | 9 | 6 | 1 |
| 200-299 | 5 | 4 | 1 | |
| 300-399 | 1 | 2 | | |
| 400-499 | | 3 | | |
| 500-749 | | 3 | | |
| 750-999 | | 2 | | |
| 1,000-1,499 | | 3 | | |
| 1,500-1,999 | | 1 | | |

Source: República de Panamá, Censos de 1960, Vol. 1.

TABLE 7

AGRICULTURAL LAND-USE[1], PANAMA, 1960
(By Province)

| Province | Total Area under Cultivation[2] (Acres) | (% of Province) | Rice (Acres) | Maize (Acres) |
|---|---|---|---|---|
| Bocas del Toro | 116,912 | 2.8 | 2,209 | 2,763 |
| Coclé | 451,486 | 19.0 | 40,222 | 24,073 |
| Colón | 138,588 | 4.0 | 11,886 | 13,803 |
| Chiriquí | 1,398,287 | 34.0 | 98,559 | 76,713 |
| Darien | 73,108 | 0.9 | 7,703 | 8,220 |
| Herrera | 467,927 | 41.0 | 37,393 | 33,957 |
| Los Santos | 768,656 | 42.3 | 55,206 | 72,652 |
| Panama | 483,329 | 9.1 | 46,624 | 54,548 |
| Veraguas | 867,652 | 16.6 | 116,809 | 76,539 |

(1) Only the two major subsistance crops are shown separately.
(2) Includes sown pasture.

Source: República de Panamá, Censos Nacionales de 1960.

TABLE 8

CATTLE AND GRAZING LAND, PANAMA, 1950 AND 1960
(By Province)

| Province | Number of Cattle | | Land Used for Grazing (% of total area of Province) | |
|---|---|---|---|---|
| | 1950 | 1960 | 1950 | 1960 |
| Bocas del Toro | 4,829 | 8,623 | 2.0 | 4.7 |
| Coclé | 57,395 | 70,613 | 19.2 | 28.6 |
| Colón | 7,286 | 9,708 | 2.9 | 7.4 |
| Chiriquí | 162,581 | 234,447 | 33.0 | 42.4 |
| Darien | 1,888 | 3,586 | 0.5 | 1.5 |
| Herrera | 80,707 | 90,236 | 42.5 | 57.0 |
| Los Santos | 117,622 | 158,963 | 34.7 | 54.9 |
| Panama | 29,630 | 53,061 | 9.4 | 18.6 |
| Veraguas | 108,085 | 131,698 | 11.5 | 26.0 |

Source: República de Panamá, Censos Nacionales: 1950; 1960.

TABLE 9

ALTO LINO (Boquete)
TEMPERATURE AND RELATIVE HUMIDITY
April 2-8, 1963 (Dry-Wet Season Transition)

| | Forest | | | | Clearing | | | |
|---|---|---|---|---|---|---|---|---|
| | 0600 | 1200 | 1800 | 2400 | 0600 | 1200 | 1800 | 2400 |
| April 2 | | | | | | | | |
| °F | - | 66 | 62 | 59 | - | 70 | 65 | 60 |
| %RH | - | 90 | 100 | 100 | - | 68 | 80 | 100 |
| April 3 | | | | | | | | |
| °F | 57 | 70 | 64 | 63 | 56 | 78 | 62 | 60 |
| %RH | 100 | 68 | 100 | 100 | 90 | 64 | 100 | 100 |
| April 4 | | | | | | | | |
| °F | 63 | 69 | 62 | 59 | 60 | 74 | 59 | 54 |
| %RH | 100 | 75 | 100 | 100 | 100 | 64 | 100 | 100 |
| April 5 | | | | | | | | |
| °F | 61 | 67 | 65 | 64 | 56 | 76 | 62 | 59 |
| %RH | 100 | 100 | 100 | 100 | 100 | 64 | 100 | 100 |
| April 6 | | | | | | | | |
| °F | 64 | 66 | 66 | 62 | 59 | 66 | 60 | 58 |
| %RH | 100 | 100 | 100 | 100 | 100 | 70 | 100 | 100 |
| April 7 | | | | | | | | |
| °F | 60 | 67 | 66 | 64 | 54 | 76 | 64 | 60 |
| %RH | 100 | 100 | 100 | 100 | 100 | 75 | 100 | 100 |
| April 8 | | | | | | | | |
| °F | 61 | 68 | 66 | 64 | 56 | 75 | 64 | 59 |
| %RH | 100 | 100 | 100 | 100 | 100 | 80 | 100 | 100 |

TABLE 10 (Part 1)

PONUGA (Finca Alba)
TEMPERATURE AND RELATIVE HUMIDITY
March 2-8, 1963 (Dry Season)

| | Forest | | | | Clearing | | | |
|---|---|---|---|---|---|---|---|---|
| | 0600 | 1200 | 1800 | 2400 | 0600 | 1200 | 1800 | 2400 |
| March 2 | | | | | | | | |
| °F | - | - | 80 | 68 | - | 96 | 83 | 70 |
| %RH | - | - | 75 | 98 | - | 44 | 59 | 78 |
| March 3 | | | | | | | | |
| °F | 65 | 87 | 80 | 64 | 66 | 97 | 81 | 68 |
| %RH | 100 | 42 | 54 | 98 | 80 | 38 | 55 | 76 |
| March 4 | | | | | | | | |
| °F | 66 | 89 | 78 | 70 | 72 | 95 | 80 | 74 |
| %RH | 100 | 48 | 88 | 100 | 68 | 40 | 70 | 78 |
| March 5 | | | | | | | | |
| °F | 69 | 80 | 76 | 69 | 72 | 91 | 77 | 72 |
| %RH | 100 | 62 | 92 | 100 | 76 | 50 | 78 | 78 |
| March 6 | | | | | | | | |
| °F | 67 | 84 | 68 | 66 | 70 | 97 | 72 | 69 |
| %RH | 100 | 60 | 100 | 100 | 78 | 42 | 78 | 78 |
| March 7 | | | | | | | | |
| °F | 63 | 82 | 76 | 66 | 75 | 94 | 77 | 68 |
| %RH | 100 | 47 | 94 | 98 | 70 | 38 | 76 | 78 |
| March 8 | | | | | | | | |
| °F | 62 | 84 | 72 | 67 | 70 | 98 | 74 | 68 |
| %RH | 100 | 46 | 100 | 100 | 70 | 38 | 76 | 78 |

TABLE 10 (Part 2)

PONUGA (Finca Alba)
TEMPERATURE AND RELATIVE HUMIDITY
May 13-19,1963 (Wet Season)

| | Forest | | | | Clearing | | | |
|---|---|---|---|---|---|---|---|---|
| | 0600 | 1200 | 1800 | 2400 | 0600 | 1200 | 1800 | 2400 |
| May 13 | | | | | | | | |
| °F | - | 90 | 88 | 74 | - | 98 | 84 | 71 |
| %RH | - | 68 | 75 | 100 | - | 48 | 70 | 100 |
| May 14 | | | | | | | | |
| °F | 70 | 82 | 80 | 75 | 78 | 95 | 81 | 74 |
| %RH | 100 | 60 | 78 | 100 | 100 | 42 | 70 | 100 |
| May 15 | | | | | | | | |
| °F | 73 | 82 | 80 | 75 | 72 | 90 | 78 | 73 |
| %RH | 100 | 72 | 86 | 100 | 100 | 62 | 88 | 100 |
| May 16 | | | | | | | | |
| °F | 73 | 83 | 78 | 73 | 70 | 94 | 74 | 72 |
| %RH | 100 | 64 | 100 | 100 | 100 | 54 | 100 | 100 |
| May 17 | | | | | | | | |
| °F | 71 | 82 | 75 | 74 | 68 | 93 | 74 | 72 |
| %RH | 100 | 75 | 100 | 100 | 100 | 55 | 100 | 100 |
| May | | | | | | | | |
| May 18 | | | | | | | | |
| °F | 73 | 82 | 77 | 75 | 70 | 92 | 78 | 72 |
| %RH | 100 | 75 | 100 | 100 | 100 | 54 | 100 | 100 |
| May 19 | | | | | | | | |
| °F | 73 | 83 | 81 | 78 | 72 | 92 | 82 | 78 |
| %RH | 100 | 72 | 100 | 100 | 100 | 54 | 72 | 85 |

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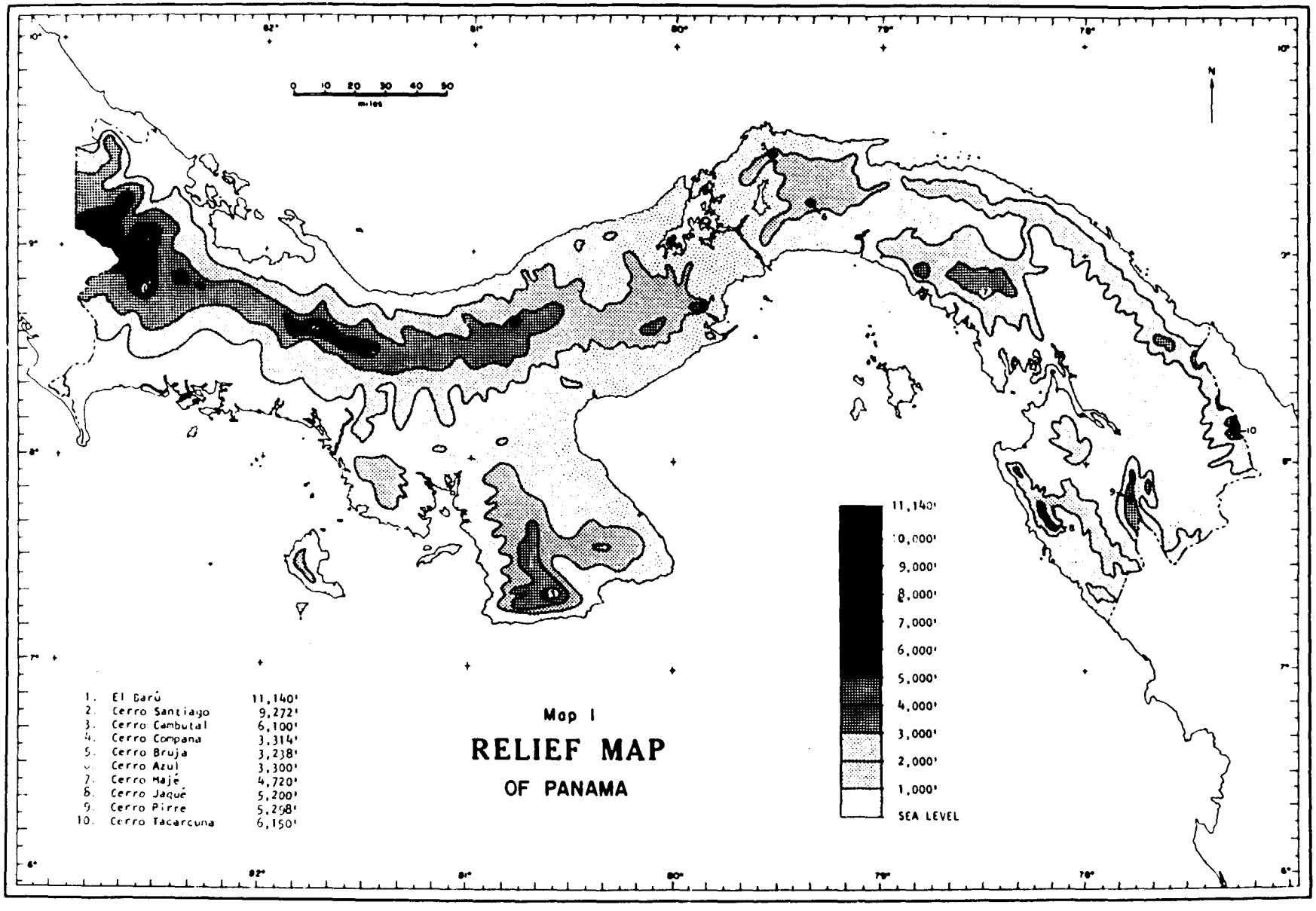
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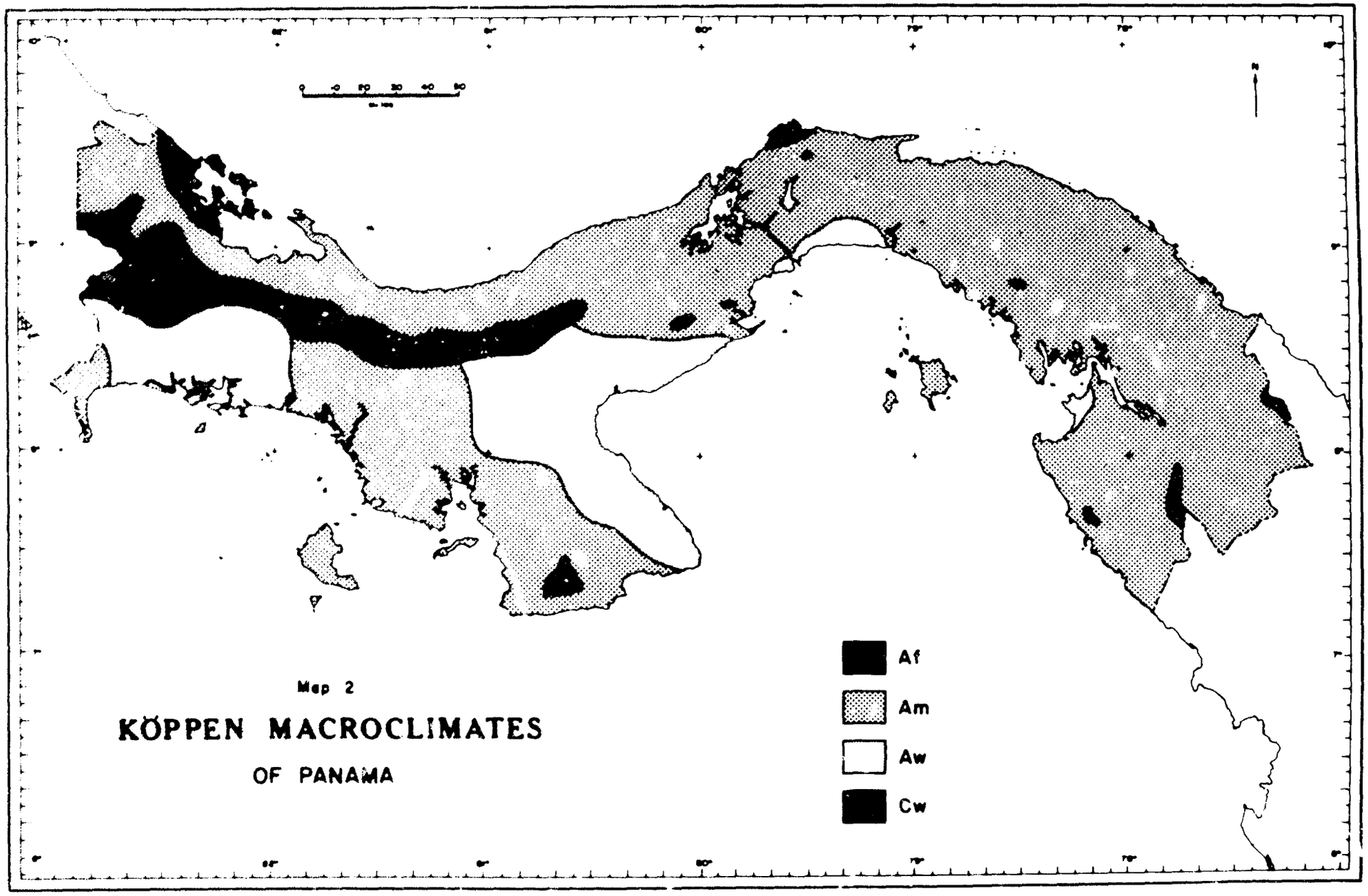
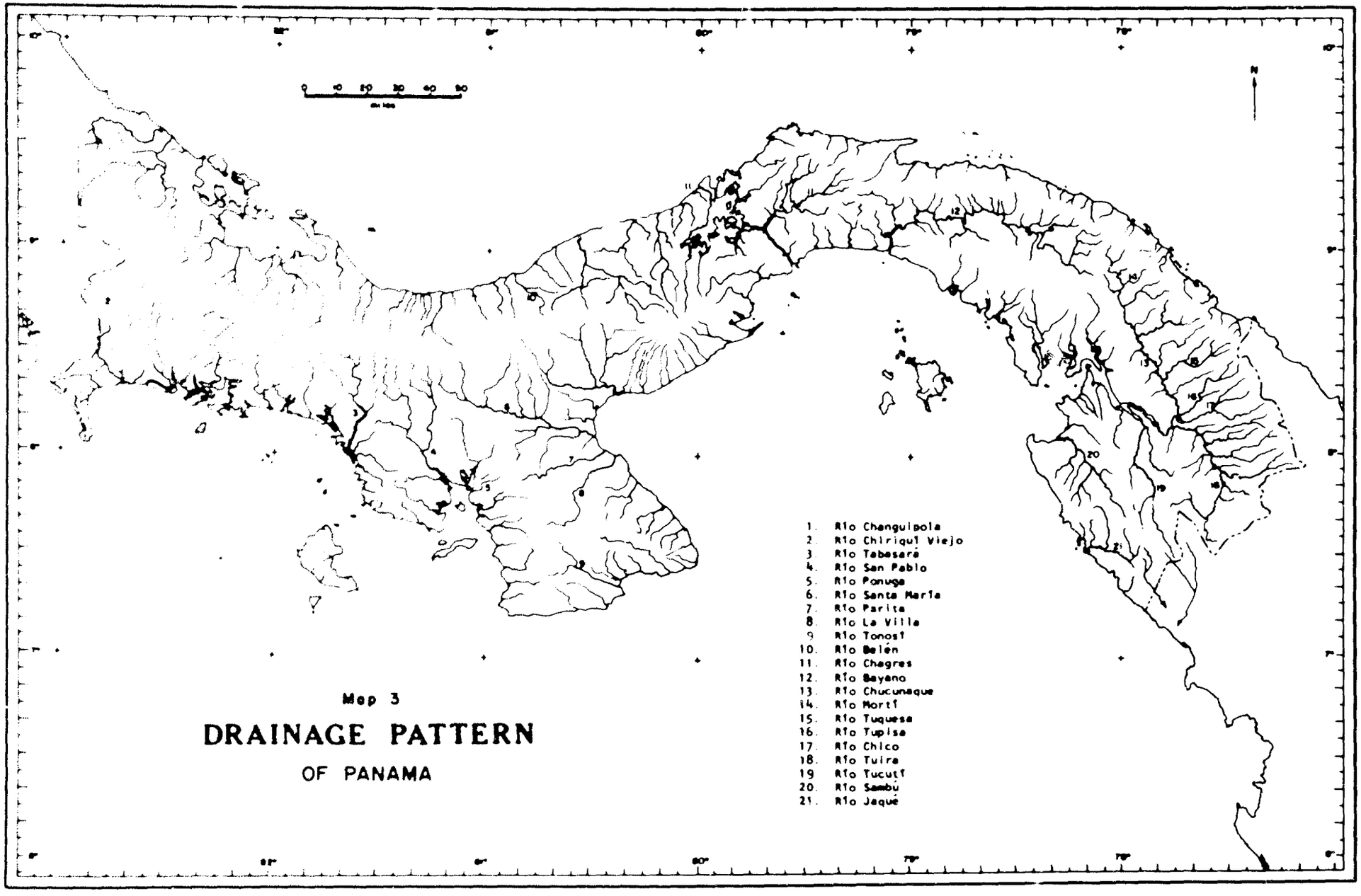
miles
N
11,140'
10,000'
9,000'
8,000'
7,000'
6,000'
5,000'
4,000'
3,000'
2,000'
1,000'
SEA LEVEL
1. El Barú 11,140'
2. Cerro Santiago 9,272'
3. Cerro Cambutal 6,100'
4. Cerro Campana 3,314'
5. Cerro Bruja 3,238'
6. Cerro Azul 3,300'
7. Cerro Majé 4,720'
8. Cerro Jaqué 5,200'
9. Cerro Pirre 5,298'
10. Cerro Tacarcuna 6,150'
Map I
RELIEF MAP
OF PANAMA




Map 2

## KÖPPEN MACROCLIMATES

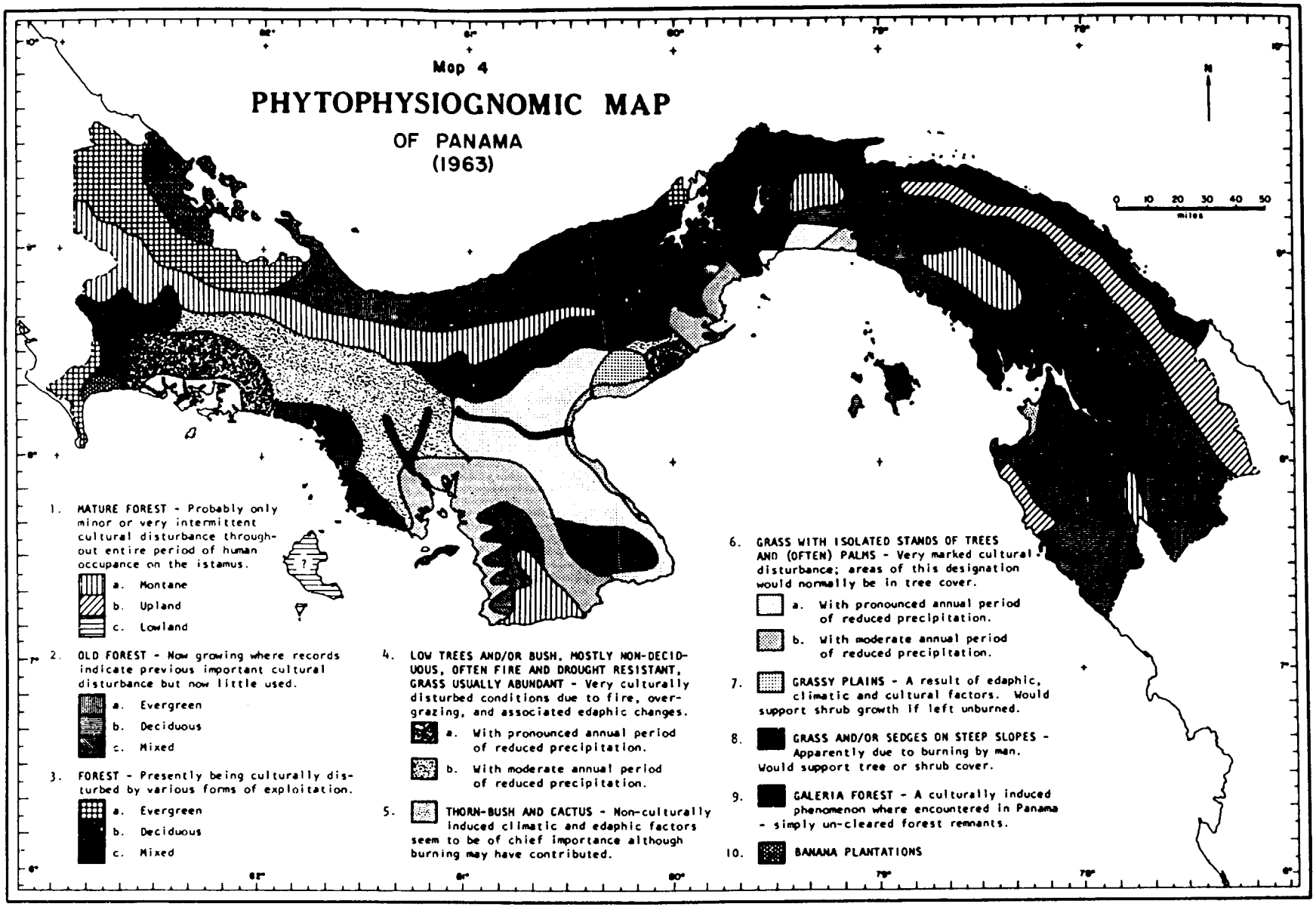
OF PANAMA

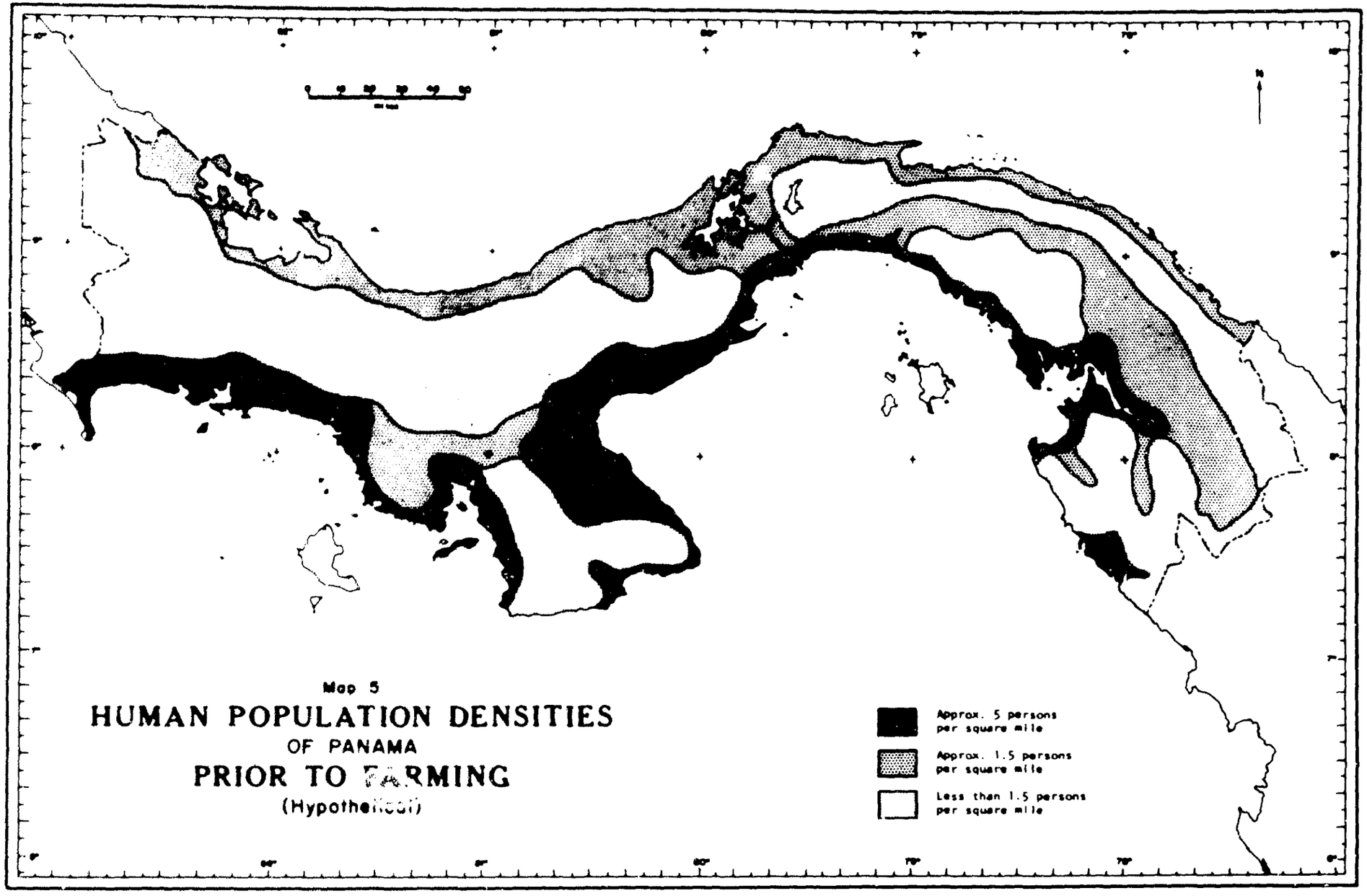



Map 3

# DRAINAGE PATTERN

## OF PANAMA

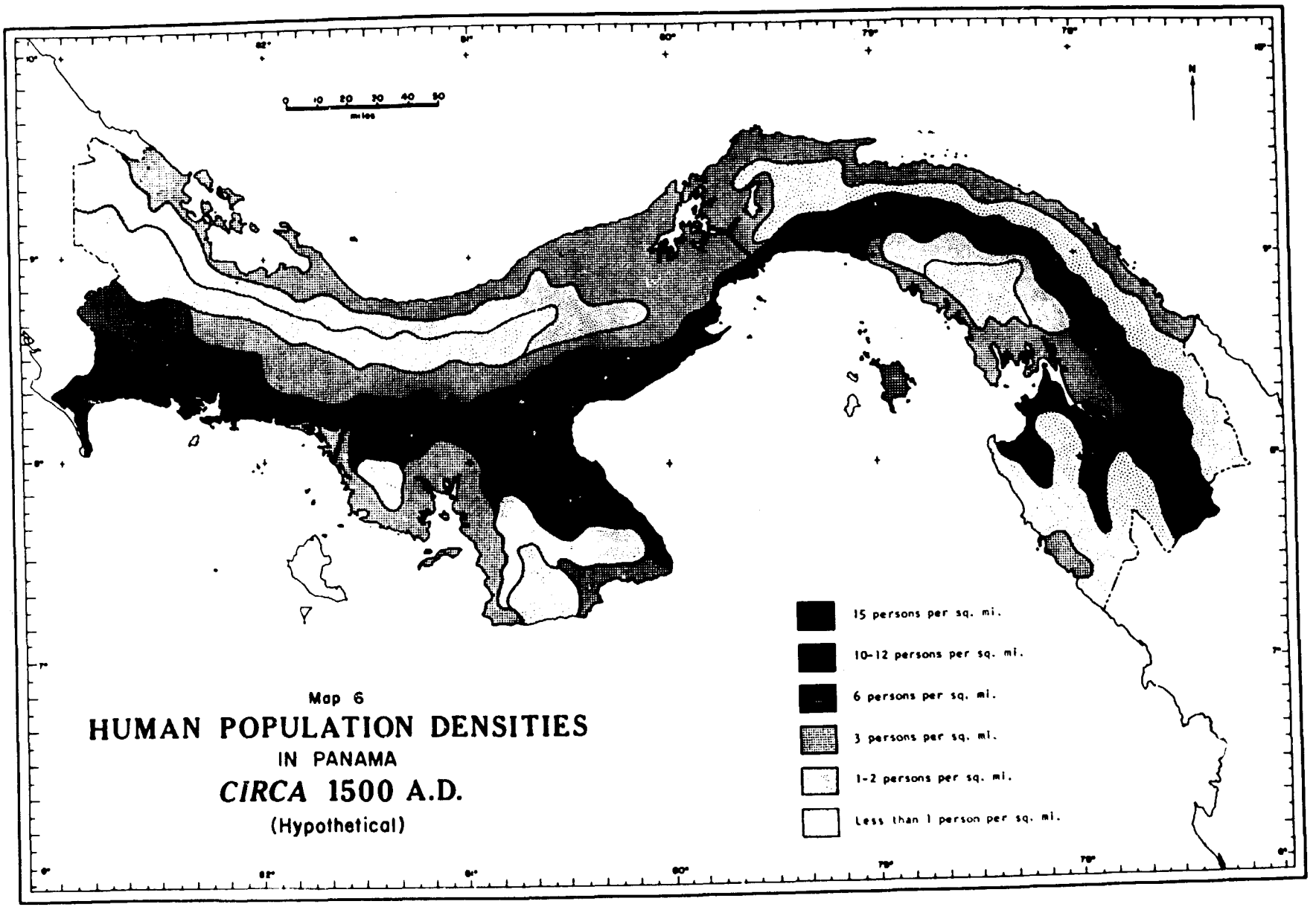

Map 4
PHYTOPHYSIOGNOMIC MAP
OF PANAMA
(1963)
N
0 10 20 30 40 50
miles
1. MATURE FOREST - Probably only minor or very intermittent cultural disturbance throughout entire period of human occupance on the istamus.
a. Montane
b. Upland
c. Lowland
2. OLD FOREST - Now growing where records indicate previous important cultural disturbance but now little used.
a. Evergreen
b. Deciduous
c. Mixed
3. FOREST - Presently being culturally disturbed by various forms of exploitation.
a. Evergreen
b. Deciduous
c. Mixed
4. LOW TREES AND/OR BUSH, MOSTLY NON-DECIDUOUS, OFTEN FIRE AND DROUGHT RESISTANT, GRASS USUALLY ABUNDANT - Very culturally disturbed conditions due to fire, overgrazing, and associated edaphic changes.
a. With pronounced annual period of reduced precipitation.
b. With moderate annual period of reduced precipitation.
5. THORN-BUSH AND CACTUS - Non-culturally induced climatic and edaphic factors seem to be of chief importance although burning may have contributed.
6. GRASS WITH ISOLATED STANDS OF TREES AND (OFTEN) PALMS - Very marked cultural disturbance; areas of this designation would normally be in tree cover.
a. With pronounced annual period of reduced precipitation.
b. With moderate annual period of reduced precipitation.
7. GRASSY PLAINS - A result of edaphic, climatic and cultural factors. Would support shrub growth if left unburned.
8. GRASS AND/OR SEDGES ON STEEP SLOPES - Apparently due to burning by man. Would support tree or shrub cover.
9. GALERIA FOREST - A culturally induced phenomenon where encountered in Panama - simply un-cleared forest remnants.
10. BANANA PLANTATIONS




Map 5

# HUMAN POPULATION DENSITIES OF PANAMA PRIOR TO FARMING

(Hypothetical)



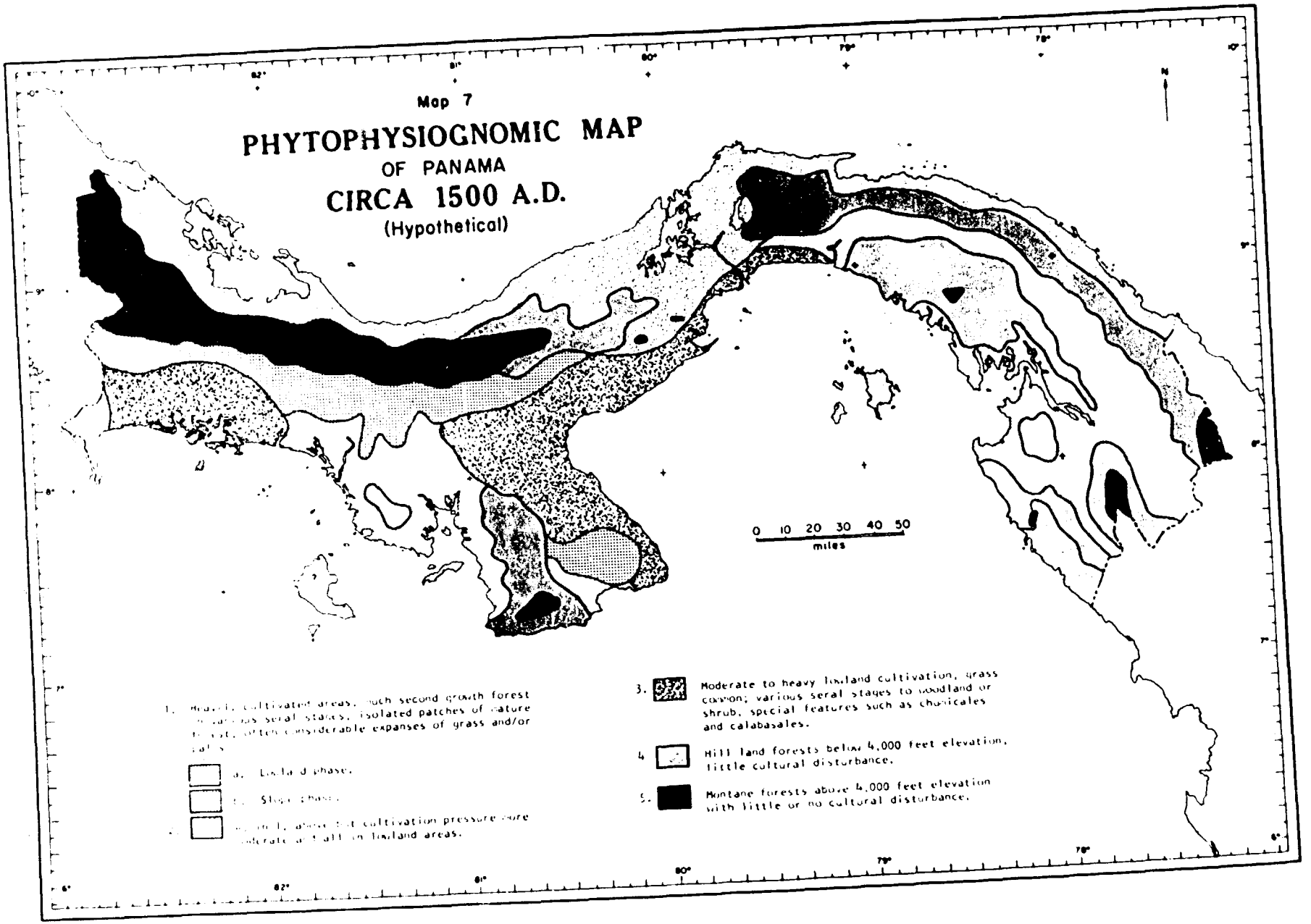

Map 6

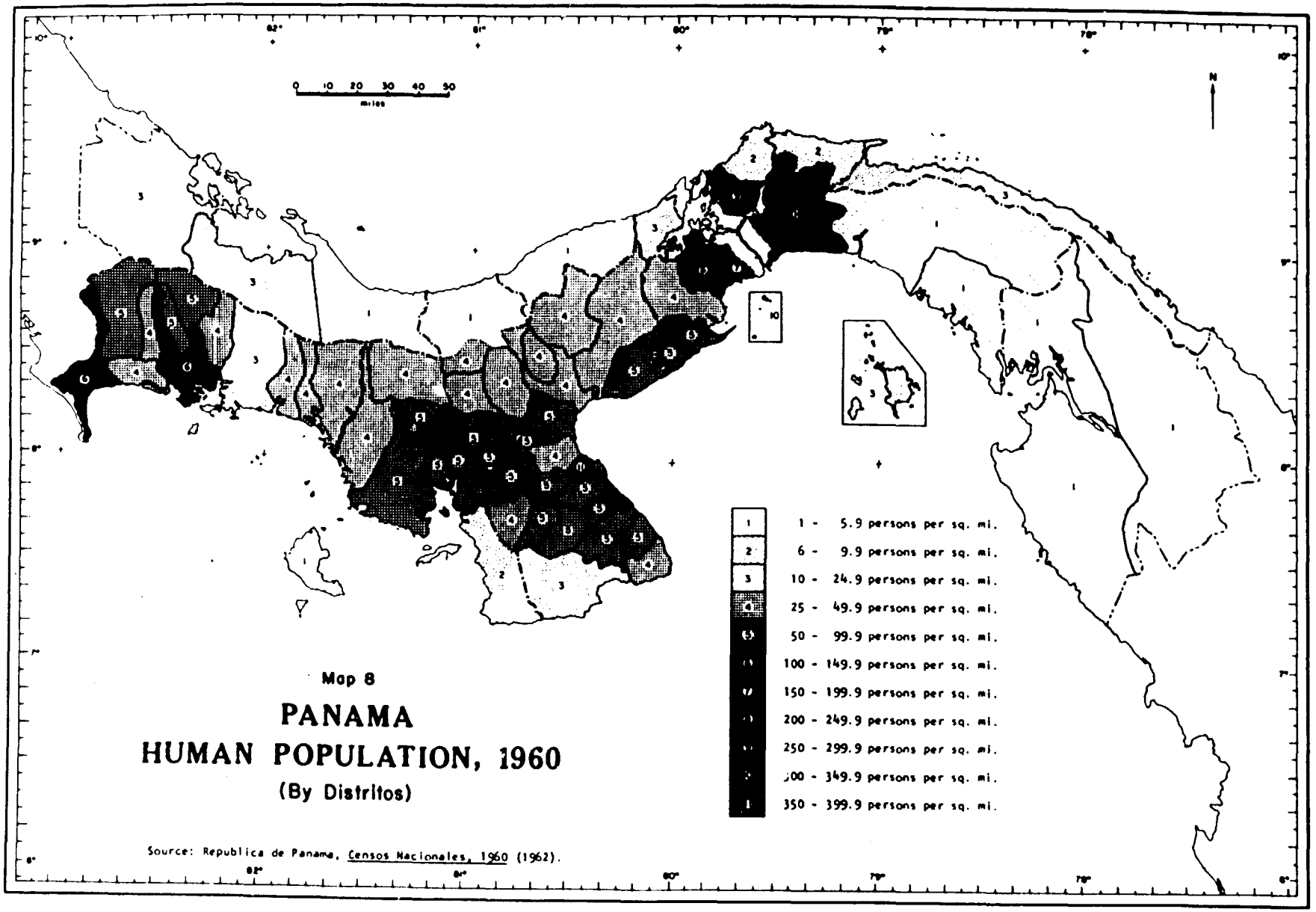
# HUMAN POPULATION DENSITIES

IN PANAMA

## *CIRCA* 1500 A.D.

(Hypothetical)


Map 7
PHYTOPHYSIOGNOMIC MAP
OF PANAMA
CIRCA 1500 A.D.
(Hypothetical)
N
0 10 20 30 40 50
miles
3. Moderate to heavy lowland cultivation, grass common; various seral stages to woodland or shrub, special features such as chunicales and calabasales.
4 Hill land forests below 4,000 feet elevation, little cultural disturbance.
5. Montane forests above 4,000 feet elevation with little or no cultural disturbance.




Map 8

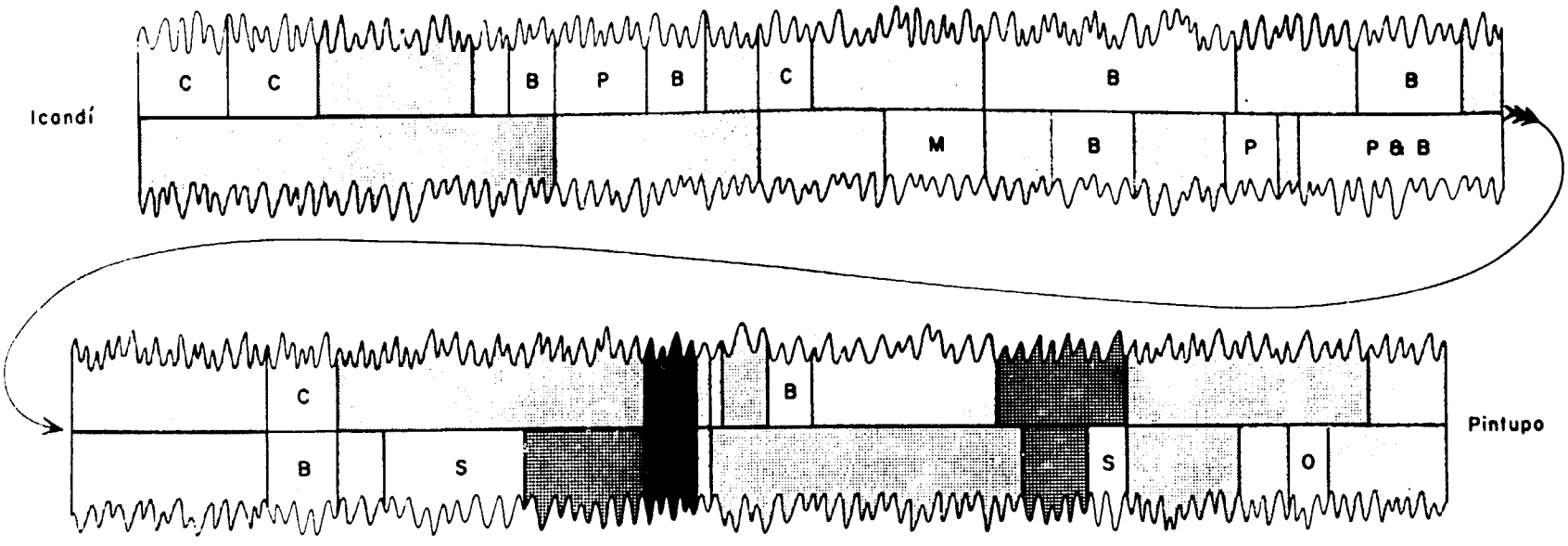
# PANAMA
# HUMAN POPULATION, 1960
## (By Distritos)

Source: Republica de Panama, Censos Nacionales, 1960 (1962).

Map 9

# LAND USE IN THE BAYANO CUNA REGION, PANAMA

## TRAIL TRANSECT BETWEEN THE VILLAGES OF ICANDI AND PINTUPO




CROPS

B Bananas

C Coffee

M Maize

O Oranges

P Plantains

S Sugar Cane

SECOND GROWTH AGE CLASSES

- 1 year or less
- 1-2 years
- 2-3 years
- 3-4 years
- 4-5 years
- 5-6 years
- 6-7 years

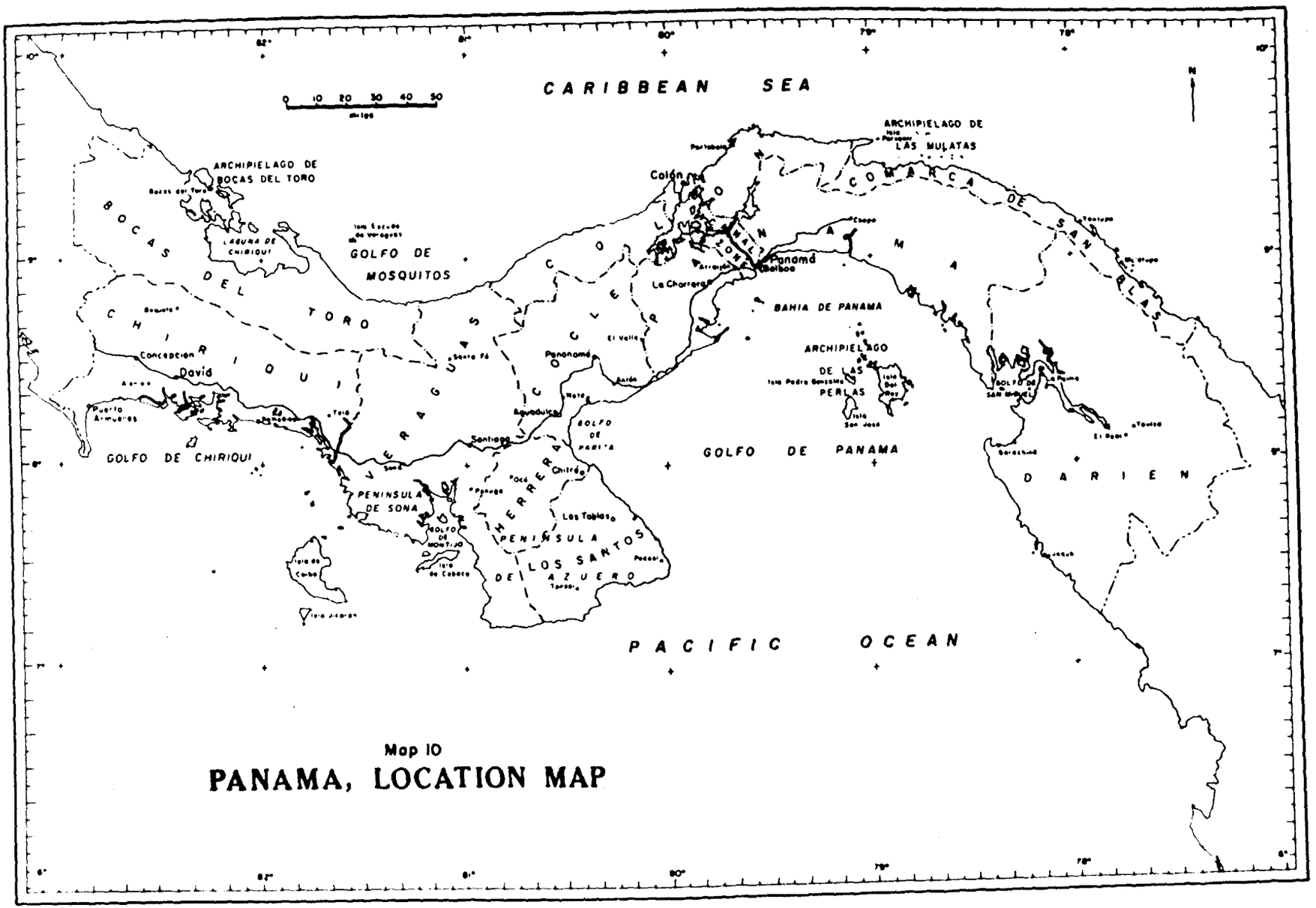
0 100 500 1000

FEET

NOTES:

In areas planted to coffee, balsa, Ochroma spp., is a common shade tree.

Field size is extremely variable and no system of land measure is employed. Therefore only the front dimensions are shown. The trail is shown as a straight line for cartographic convenience.




Map 10

# PANAMA, LOCATION MAP

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*(Security classification of title, body of abstract and indexing annotation must be entered when the overall report is classified)*

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The Influence of Contemporary Man on the Zoogeography of the Panama Land Bridge, Panama

4. DESCRIPTIVE NOTES (Type of report and inclusive dates)

Final Report

5. AUTHOR(S) (Last name, first name, initial)

Bennett, Charles F.

| 6. REPORT DATE | 7a. TOTAL NO. OF PAGES | 7b. NO. OF REFS |
|---|---|---|
| February 14, 1965 | 164 | 113 |

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The biophysical geography of the Republic of Panama is summarized. There are detailed discussions of pre-historic and historic human ecology on the isthmus with emphasis given to exploitive activities and how they relate to biotic disturbances and alterations. It is shown that man must have been in the isthmian area nearly 20 thousand years ago and that his activities, first as a food gatherer and later as a food producer and gatherer, have markedly influenced the vegetation cover and the faunal patterns on the isthmus. It is posited that the environmental influence was sufficiently great in pre-historic times to have played a significant role in certain faunal dispersals over the land bridge which connects North and South America. The Spanish invasion in the 16th century resulted in a drastic decrease in human population which led to the reestablishment of forest cover over large parts of the isthmus and, probably, an alteration of some of the faunal patterns which obtained at the time of European contact. The imposition of new land-use patterns and the growth of human populations in recent years have led again to major tree removal and faunal impoverishment. The redistribution of human population particularly in the region of the Canal has resulted in major forest removal and the creation of a new barrier to the dispersal of certain forest faunal elements. On the other hand, the changed conditions have favored the dispersal of faunal elements which are adapted to grass lands and/or second growth conditions.

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